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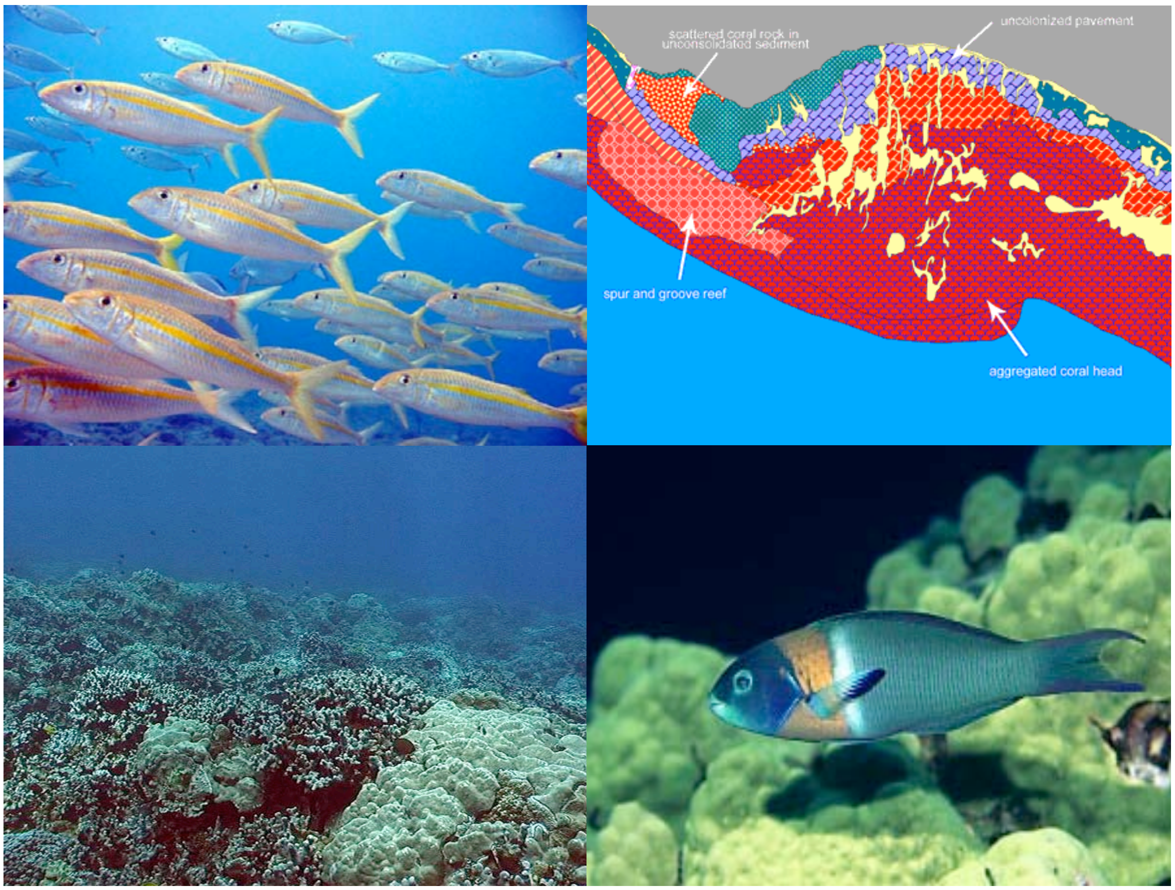

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Fish Habitat Utilization Patterns and Evaluation of the Efficacy of Marine Protected Areas in Hawaii: Integration of NOAA Digital Benthic Habitat Mapping and Coral Reef Ecological Studies

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EXECUTIVE SUMMARY

Over the past four decades, the state of Hawaii has developed a system of eleven Marine Life Conservation Districts (MLCDs) to conserve and replenish marine resources around the state. Initially established to provide opportunities for public interaction with the marine environment, these MLCDs vary in size, habitat quality, and management regimes, providing an excellent opportunity to test hypotheses concerning marine protected area (MPA) design and function using multiple discreet sampling units. NOAA/NOS/NCCOS/Center for Coastal Monitoring and Assessment's Biogeography Team developed digital benthic habitat maps for all MLCD and adjacent habitats. These maps were used to evaluate the efficacy of existing MLCDs for biodiversity conservation and fisheries replenishment, using a spatially explicit stratified random sampling design. Coupling the distribution of habitats and species habitat affinities using GIS technology elucidates species habitat utilization patterns at scales that are commensurate with ecosystem processes and is useful in defining essential fish habitat and biologically relevant boundaries for MPAs.

Analysis of benthic cover validated the *a priori* classification of habitat types and provided justification for using these habitat strata to conduct stratified random sampling and analyses of fish habitat utilization patterns. Results showed that the abundance and distribution of species and assemblages exhibited strong correlations with habitat types. Fish assemblages in the colonized and uncolonized hardbottom habitats were found to be most similar among all of the habitat types. Much of the macroalgae habitat sampled was macroalgae growing on hard substrate, and as a result showed similarities with the other hardbottom assemblages. The fish assemblages in the sand habitats were highly variable but distinct from the other habitat types.

Management regime also played an important role in the abundance and distribution of fish assemblages. MLCDs had higher values for most fish assemblage characteristics (e.g. biomass, size, diversity) compared with adjacent fished areas and Fisheries Management Areas (FMAs) across all habitat types. In addition, apex predators and other targeted resources species were more abundant and larger in the MLCDs, illustrating the effectiveness of these closures in conserving fish populations. Habitat complexity, quality, size and level of protection from fishing were important determinates of MLCD effectiveness with respect to their associated fish assemblages.

The major findings of the study are highlighted below:

<u>Benthic assemblage characteristics among the study sites</u>

- Overall, the most abundant substrate type was turf algae (48% cover) followed by sand (23%), coral (16%), macroalgae (7%), coralline algae (5%), macroinvertebrates (1%), and seagrasses (<1%).
- The Oahu sites had lower coral cover and higher macroalgal cover than the Hawaii, Lanai, and Maui sites. This pattern was most apparent at Waikiki, Pupukea, and Hanauma Bay.

- Coral cover was higher in the MLCDs compared to the open access areas with FMAs between them. In contrast, macroalgae cover was lowest in the MLCDs and highest in the open access areas.
- Macroalgal taxa appeared to account for the distinctive benthic assemblages in both the colonized and uncolonized hardbottom communities.

Factors influencing fish assemblages:

- Habitat complexity was more important than protection from fishing in explaining fish biomass, species richness, and diversity. This was partially because habitat complexity was higher in MLCDs compared with adjacent open areas. Many MLCDs were selected based on their unique ecological features making it difficult to interpret the effects of habitat relative to management regime.
- Within major habitat types, species richness, biomass, and diversity were, in most cases, nominally higher in the MLCDs, followed by FMAs, and open areas.
- Overall fish biomass was 2.6 times greater in MLCDs and the Moku o Loe reserve compared to open areas.
- Among protected areas, habitat complexity was the major determinant of fish biomass.
- Depth explained most of the variability in species richness and diversity among protected areas, with deeper MLCDs having more species and higher diversity compared to shallower protected areas.
- Protected areas, FMAs, and open areas showed greater concordance in fish assemblage structure with each other than with other locations under similar management regimes
- In the protected areas, size spectra analysis indicated that both the overall size of the adult fish assemblage was larger and the larger size classes had a greater number of individuals compared with the other management regimes.

Trophic composition observations

- Primary consumers were the most abundant (numerical and biomass) trophic group among the major habitat types.
- Although overall biomass was low in the sand habitat, apex predators accounted for 60% of the biomass in this habitat, highlighting the importance of this habitat for apex predators and the need to include sand habitats into reserve design.
- The mean ratio of apex predator biomass was more than 17 times higher in protected areas relative to their paired adjacent areas open to fishing.
- Herbivore biomass in both protected and open areas showed a negative relationship with macroalgal cover.

Comparisons among protected areas in Hawaii:

- Molokini Shoals MLCD had the highest fish biomass observed among all MLCDs, followed by Old Kona Airport, Kealakekua Bay, and Hanauma Bay. Molokini also had the greatest biomass of apex predators among all areas with sharks and jacks accounting for most of the biomass.

- The largest difference in fish biomass between MLCDs and open areas was in the Hanauma Bay MLCD, where biomass was more than eight times higher than the adjacent open area. This difference is likely due to the poor habitat quality (sedimentation, coastal development, and invasive seaweeds) and high fishing pressure in the areas outside the MLCD.
- Waialea, Kealakekua, Lapakahi, Manele, and Old Kona Airport all had relatively small differences in the ratio of fish biomass inside the MLCD compared to the adjacent open areas. Lower fishing pressure and the high habitat quality outside the MLCDs may explain these relatively small differences.
- Species richness, biomass, and diversity were low at Waikiki, Moku o Loe, WaiOpae, and Waialea. The small size and shallow depth range of these protected areas limit their effectiveness for biodiversity conservation and fisheries replenishment.

Future protected area design in the main Hawaiian Islands needs to incorporate a mosaic of habitats to support viable reef fish populations. Complex habitats will harbor higher biomass and greater species richness. Shallow nearshore habitats are necessary for recruit settlement and juvenile survival, while deeper habitats are important foraging, sheltering, and spawning sites for large adults. In addition to these hardbottom habitats, sandy areas are important corridors for the movement of predators and other vagile species between hardbottom habitats. Adjacent habitats provide coral reefs with a net gain in energy through feeding guilds that shelter on the reef by day and forage in the surrounding habitats at night (Parrish 1989). The synergy of these habitats provided needed space in an otherwise crowded biotope, the coral reef (Parrish 1989).

Many MLCDs in Hawaii were initially established to support the State of Hawaii’s conservation and education objectives, not to enhance fish stocks. As a consequence, most of the MLCDs in Hawaii are currently too small to provide any fisheries benefits. Their small size and limited habitat types do not allow for the entire fish assemblage to function in a natural manner compared to larger and relatively pristine areas such as the northwestern Hawaiian Islands (NWHI). Mean fish biomass on hardbottom habitats in the main Hawaiian Island MLCDs (0.89 t ha^{-1}) is 2.7 times less than biomass in the NWHI. The biomass of predators in protected areas is also 19 times less than those observed on unfished reefs in the NWHI (Friedlander and DeMartini 2002). MLCDs currently account for much less than 1% of the total reef area of the main Hawaiian Islands. In order for these protected areas to provide any fisheries benefits, 20-30% of the reef area needs to be protected from exploitation (Sladek Nowlis and Friedlander 2005). Self-replenishment can be achieved by reserves of sufficient size to contain a substantial amount of larval dispersal, or by networking reserves at suitable distances such that propagules produced by populations in one reserve replenish populations in other reserves. An effective reserve network design will protected populations and enhance non-protected populations through larval dispersal.

Marine reserve design must consider the habitat requirements and life histories of the species of interest as well as the extent of fishing pressure in the area and the degree of enforcement. If protective areas are to be effective, they must include the diversity of habitats necessary to accommodate the wide range of fish species. The kind of approach taken in this study, which attempts to make a functional match between habitats and fishes to be preserved, seems appropriate for selection, evaluation, and management of reserves.

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Introduction

Coral reefs have always been an important component of human existence in Hawaii. These reefs once provided the majority of the protein for the Hawaiian people, and today consumptive uses of reef resources include subsistence, commercial, and recreational activities. Coastal fisheries are facing overexploitation and severe depletion on a global scale (NRC 1999, FAO 2000, Bellwood et al. 2004, Pandolfi et al. 2005) and Hawaii is no exception. This decline in fish abundance and size, particularly around the more populated areas of the state, is likely the cumulative result of years of chronic overfishing (Shomura 2004, Friedlander and DeMartini 2002). Overfishing is often cited as the primary reason for the declining resources, both by general ocean users and commercial fishers themselves (DAR 1988, Harman and Katekaru 1988, Maly and Pomroy-Maly 2003). Factors contributing to the decline of inshore fisheries include a growing human population, destruction or disturbance to habitat, introduction of new fishing techniques (inexpensive monofilament gill nets, SCUBA, GPS, power boats, sonar fish finders), and loss of traditional conservation practices (Lowe 1996, Birkeland and Friedlander 2002). Loss of important habitat due to coastal development, sedimentation and pollution, as well as the impacts of non-native aquatic organisms has further added to this decline (Friedlander et. al. 2005).

Studies are needed to evaluate the relationship between fish assemblages and their associated habitat on a scale consistent with the patterns of both the resources and their users. Management units are typically on the scale of an island or the entire state and resource evaluation should therefore be conducted on a similar scale. Limited information exists on the distributional differences of fishes at large scales around Hawaii. A seascape perspective is critical to enhance our knowledge of marine communities. Most marine investigations have been conducted at very small scales, except for a few studies on the Great Barrier Reef (Doherty 1991, Fowler et al. 1992, Thorrold and Williams 1996). Habitat characteristics are known to play an important role in affecting the structure of coral reef fishes in Hawaii (Friedlander and Parrish 1998, Friedlander et al. 2003). Most studies of the association between fish assemblages and their supporting coral reef habitat have been conducted on individual reefs or small reef tracts or embayments. Resource evaluations that are stratified by habitat will lead to more accurate, efficient, and statistically sound results.

The poor performance of conventional fisheries management has led to increased interest among marine resource managers in marine reserves-areas of the sea permanently closed to fishing and protected from other major human impacts. Marine reserves create an off-limits population, which in theory can provide greater stability in the dynamics of the exploited populations and be incorporated into a management system as a buffer against uncertainty (Sladek Nowlis and Friedlander 2005). The U.S. Coral Reef Task Force has identified MPAs as a key conservation tool to ensure the long-term viability, ecological integrity, and sustainability of the nation’s coral reefs. Results point to the fact that “no-take” marine protected areas with good habitat diversity and complexity can have a positive effect on fish standing stock. Marine reserves also have many non-fisheries benefits, such as protecting biodiversity and ecosystem structure, serving as biological reference areas, and providing opportunities for non-consumptive recreational activities. Marine reserve designs need to consider the habitat requirements and life histories of the species of interest as well as the extent of fishing pressure in the area and the degree of enforcement. If protective areas are to be effective, they must include the diversity of habitats necessary to accommodate the wide range of fish species under consideration.

The State of Hawaii has numerous marine protected areas and other marine managed areas – natural area reserves, fishery management areas, marine life conservation districts, various protective subzones, military defensive areas, and National Park coastlines. Hawaii established its first MPAs over 30 years ago. Since that time, numerous MPAs and MMAs (Marine Managed Areas) have been established with varying levels of protection ranging from complete 'no-take' areas to areas that have allowed a wide variety of activities to occur within their boundaries (Table 1). Designation of many of these areas was not based on comprehensive biological selection criteria but rather on the need to manage user conflicts, safeguard protected species, or on the wishes of local communities. Owing to the diversity of existing MPAs in Hawaii, it is critical that the efficacies of these areas are evaluated. In addition, no assessment has been initiated to assess the contributions of MPAs and MMAs to the wider region outside of the designated areas, or to the contributions to the fishery resources in exploited areas that are not protected.

The National Ocean Service, Center for Coastal Monitoring and Assessment's (CCMA) Biogeography Team has developed digital benthic habitat maps for pilot study areas in Hawaii. The integrated mapping and monitoring of coral reef ecosystems and reef fish habitat utilization patterns has been designed to help resource managers make informed decisions. Coupling the distribution of habitats and species habitat affinities using GIS technology enables the elucidation of species habitat utilization patterns for a single species and/or assemblages of animals. This integrated approach is useful in quantitatively defining essential fish habitat and defining biologically relevant boundaries of marine protected areas

By integrating spatial data into the biological sampling design, significant progress can be made towards identifying and quantifying spatial dependencies in habitat utilization by reef fishes. This design also lends itself to elucidating factors that might suggest cause for differential patterns in ontogenetic habitat selection, ergo distribution, within the available landscape. Such patterns in population and community structure are necessary and fundamental components of any intent to understand and maximize the benefits derived from a Marine Protected Area.

The keystone products used to design the reef fish ecology and assessment of ecosystem health are the digital and georeferenced NOS benthic habitat maps. In Hawaii, development of the fundamental map products is now underway and partially completed.

Objectives

By integrating assessments of the distribution and quality of habitats and associated reef fishes, NOS and its partners are attempting to provide analytical justification to define and support MPA boundaries. However, to have the capability to address the effectiveness of MPAs, the first step in this process is to define species habitat utilization patterns across varying levels of habitat quality and protection. The Hawaii Department of Land and Natural Resources has requested that NOS implement the approach taken in the USVI and Puerto Rico to aid in evaluating the designation and effectiveness of marine reserves under various management strategies. A science-based assessment of the effectiveness of Hawaii's MPA system will also support the federally mandated marine protected area (MPA) and essential fish habitat (EFH) initiatives. This approach will not only help resource managers in Hawaii evaluate existing MPAs and help design new protected areas, its will also lay the groundwork for large-scale comparisons throughout the Hawaiian archipelago, the US Pacific, and US Caribbean.

Table 1. Summary of state MLCD characteristics and the Moku o Loe University Marine Laboratory Refuge. Use = level of use as classified by DAR (DAR 1992). Protection from fishing based on regulations, not on enforcement of these regulations (Modified from Friedlander and Brown 2004).

Protected area	Acres	Year estab.	Use	Protection from fishing	Permitted activities
Oahu					
Hanauma Bay	101	1967	High	High	Complete no-take
Pupukea	179	1983 modified 2003	Mod	Mod	Pole-&-line from shore (Waimea Bay only) Harvest of limu (seaweed) Akule (Nov.-Dec.) & opelu (Aug.-Sep.) – Waimea Bay only
Waikiki	78	1988	High	High	Complete no-take
Moku o Loe - Univ. Marine Lab. Refuge	73	1967	Low	High	Scientific collecting and propagation
Hawaii					
Kealakekua Bay	305	1969	High	Mod	Hook & line – 60% of MLCD Thrownet – 60% of MLCD Akule & opelu – 60% of MLCD Crustaceans – 60% MLCD
Lapakahi	133	1979	Low	Low	Hook & line – 90% of MLCD Thrownet – 90% of MLCD Liftnet for opelu – 90% of MLCD
Waialea Bay	35	1985	Low	Low	Hook & line Netting
Old Kona Airport	262	1992	Mod	Mod	Thrownet and pole and line from shore, sea urchin collecting without scuba from June 1 to October 1
WaiOpae	65	2003	Mod	High	Complete no-take
Lanai					
Manele-Hulopoe	276	1976	Mod	Mod	Hook & line (shore) – 100% of MLCD All fishing except spear, trap, and net (other than thrownet) – 50% of MLCD
Maui					
Molokini Shoal	88	1977	High	High	Trolling in 60% of MLCD
Honolua-Mokuleia Bay	45	1978	Mod	High	Complete no-take

Methods

Benthic habitat mapping

The National Oceanic and Atmospheric Administration (NOAA) acquired and visually interpreted orthorectified aerial photography for the near-shore waters (to 25 meters depth) of parts of the main Hawaiian Islands (Coyne et al. 2003, NOAA/NOS 2003). Features visible in the aerial photographs were mapped directly into a geographic information system (GIS). Visual interpretation of the photographs was guided by a hierarchical classification scheme that defined and delineated benthic polygon types based on insular-shelf zones and habitat structures of the benthic community. Zones describe the insular-shelf location (inner lagoon, outer lagoon, bank-shelf), whereas habitat structure (hereafter "structure") includes the cover type (reef, submerged vegetation, unconsolidated sediments, etc.) of the benthic community. The major product of this effort is a series of GIS-based benthic habitat maps that are characterized by a high degree of spatial and thematic accuracy. The hierarchical spatial structure underlying the habitat classifications were explicitly designed to include ecologically-relevant locational (backreef, forereef, lagoon, etc.) and typological (patch reef, spur and groove, colonized pavement, etc.) strata, thereby creating an analytical construct within which nuances of community structure, such as resource distribution, abundance, and habitat utilization, can be tested and resolved.

Twenty-seven distinct and non-overlapping habitat types were identified that could be mapped by visual interpretation of remotely collected imagery (Table 2). Habitats or features that cover areas smaller than the minimum mapping unit of one acre were not considered. For example, sand halos surrounding patch reefs are too small to be mapped independently. Habitat refers only to each benthic community's substrate and/or cover type and does not address location on the shelf. Habitats are defined in a collapsible hierarchy ranging from four broad classes (unconsolidated sediment, submerged vegetation, coral reef and hardbottom, and other), to more detailed categories (e.g., emergent vegetation, seagrass, algae, individual patch reefs, uncolonized volcanic rock), to patchiness of some specific features (e.g., 50-90 percent cover of macroalgae).

Sampling locations

Locations of assessment sites were determined using a stratified random sampling approach. Random points were assigned in each of the four major habitat strata (colonized hardbottom [CHB], uncolonized hardbottom [UCH], unconsolidated sediment [sand], and macroalgae [MAC]) in Arcview. Location points in either latitude and longitude or UTM coordinates were downloaded from Arcview into a GPS as waypoints for use in the field. Sampling was conducted in all 11 MLCDs (Fig. 1), the University Marine Laboratory Refuge (Moku o Loe), and adjacent habitats.

A field team consisting of 2 divers navigated to waypoints using GPS, they then marked the location with a lead weight and float and accurately established the location using GPS measurements. Direction of each transect was determined randomly along the isobath of that point except in cases where that direction caused the transect to traverse multiple habitats. In those situations, transects were run within a habitat polygon at a similar isobath strata. Divers descend together; with diver 1 carrying a 25 m transect line and diver 2 carrying a video camera and rugosity chain. Diver 1 began a 25 x 5 m fish transect starting at the marked waypoint and moved along the depth contour. As the fish count diver started his/her count, he or she visualized out to the end of the transect and enumerated all individuals that were potentially leaving the census area. In this manner, we were able to partially account for the behavior that targeted species acquire in areas that are frequented by spearfishers. The fish count method is described in detail below. As diver 1 laid out transect line, diver 2 conducted benthic surveys. Once diver 1 completed the fish transect, he/she conducted rugosity measurements as described below.

Fish sampling methodology

Fish assemblages at each location were assessed using standard underwater visual belt transect survey methods (VE Brock 1954; RE Brock 1982). A diver swam each 25m x 5m transect at a constant speed (~ 15 min/transect) and identified to the lowest possible taxon, all fishes visible within 2.5 m to either side of the centerline (125 m^2 transect area). Nomenclature followed Randall (1996). Total length (TL) of fish was estimated to the nearest centimeter. Length estimates of fishes from visual censuses were converted to weight using the following length-weight conversion: $W = aSL^b$ where the parameters a and b are constants for the allometric growth equation and SL is standard length in mm and W is weight in grams. Total length was converted to standard length (SL) by multiplying standard length to total length-fitting parameters obtained from FishBase (WWW.fishbase.org). Length-weight fitting parameters were available for 150 species commonly observed on visual fish transects in Hawaii (Hawaii Cooperative Fishery Research Unit unpublished data). This was supplemented by using information from other published and web-based sources. In the cases where length-weight information did not exist for a given species, the parameters from similar bodied congeners were used. All biomass estimates were converted to metric tons per hectare (t/ha) to facilitate comparisons with other studies in Hawaii. Finally, fish taxa were categorized into three trophic categories (herbivores, secondary consumers, and apex predators) according to various published sources and FishBase (WWW.fishbase.org).

Fish sample size optimization analysis

Optimal sample size was determined for number of species and number of individuals per transect among the four major habitat types surveyed in the study area. A technique developed by Bros and Cowell (1987) using the standard error of the mean to resolve statistical power was used to determine the number of samples needed using number of species and number of individuals. This method uses a Monte Carlo simulation procedure to generate a range of sample sizes versus power. The sample size at which further increase in sample size does not substantially increase power (decreasing SEM) is taken as the minimum suitable number of samples. For number of species per transect, high and low standard error of the mean began to level off and converge at ca. four samples in the colonized hardbottom habitat and unconsolidated sediment habitat and ca. eight samples for the macroalgae and uncolonized hardbottom habitats (Fig. 2 and 3). For number of individuals per transect, high and low standard error of the mean began to converge at six samples in the unconsolidated sediment habitat and nine samples in the macroalgae habitat. Given these results, 9 to10 samples per habitat appeared to be adequate to control the standard error of the mean for number of individuals and number of species per transect.

Table 2. NOAA hierarchical benthic habitat classification scheme (Coyne et al. 2001).

- Unconsolidated Sediment (0%-<10% submerged vegetation)
  - Mud
  - Sand
- Submerged Vegetation
  - Seagrass
    - Continuous Seagrass (90%-100% Cover)
    - Patchy (Discontinuous) Seagrass (50%-<90% Cover)
    - Patchy (Discontinuous) Seagrass (10%-50% Cover)
  - Macroalgae (fleshy and turf)
    - Continuous Macroalgae (90%-100% Cover)
    - Patchy (Discontinuous) Macroalgae (50%-<90% Cover)
    - Patchy (Discontinuous) Macroalgae (10%-<50% Cover)
- Coral Reef and Hardbottom
  - Coral Reef and Colonized Hardbottom
    - Linear Reef
    - Aggregated Coral
    - Spur and Groove
    - Individual Patch Reef
    - Aggregated Patch Reef
    - Scattered Coral/Rock in Unconsolidated Sediment
    - Colonized Pavement
    - Colonized Volcanic Rock/Boulder
    - Colonized Pavement with Sand Channels
  - Uncolonized Hardbottom
    - Reef Rubble
    - Uncolonized Pavement
    - Uncolonized Volcanic Rock/Boulder
    - Uncolonized Pavement with Sand Channels
- Encrusting/Coralline Algae
    - Continuous Encrusting/Coralline Algae (90%-100% Cover)
    - Patchy (Discontinuous) Encrusting/Coralline Algae (50%-<90% Cover)
    - Patchy (Discontinuous) Encrusting/Coralline Algae (10%-<50% Cover
- Other Delineations
  - Land
  - Emergent Vegetation
  - Artificial
  - Unknown

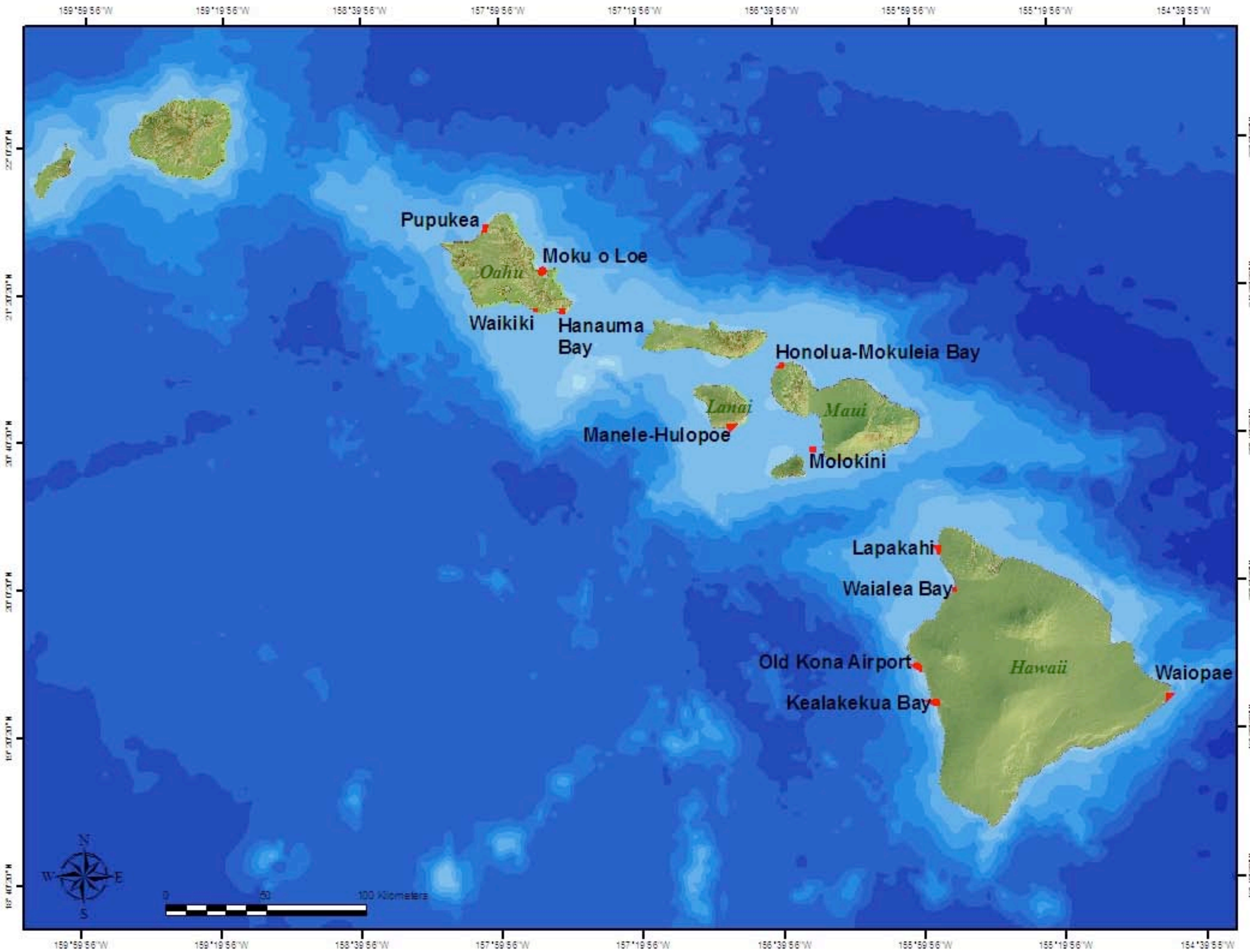

Figure 1. Locations of Marine Life Conservation Districts and the University of Hawaii Marine Laboratory Refuge (Moku o Loe).

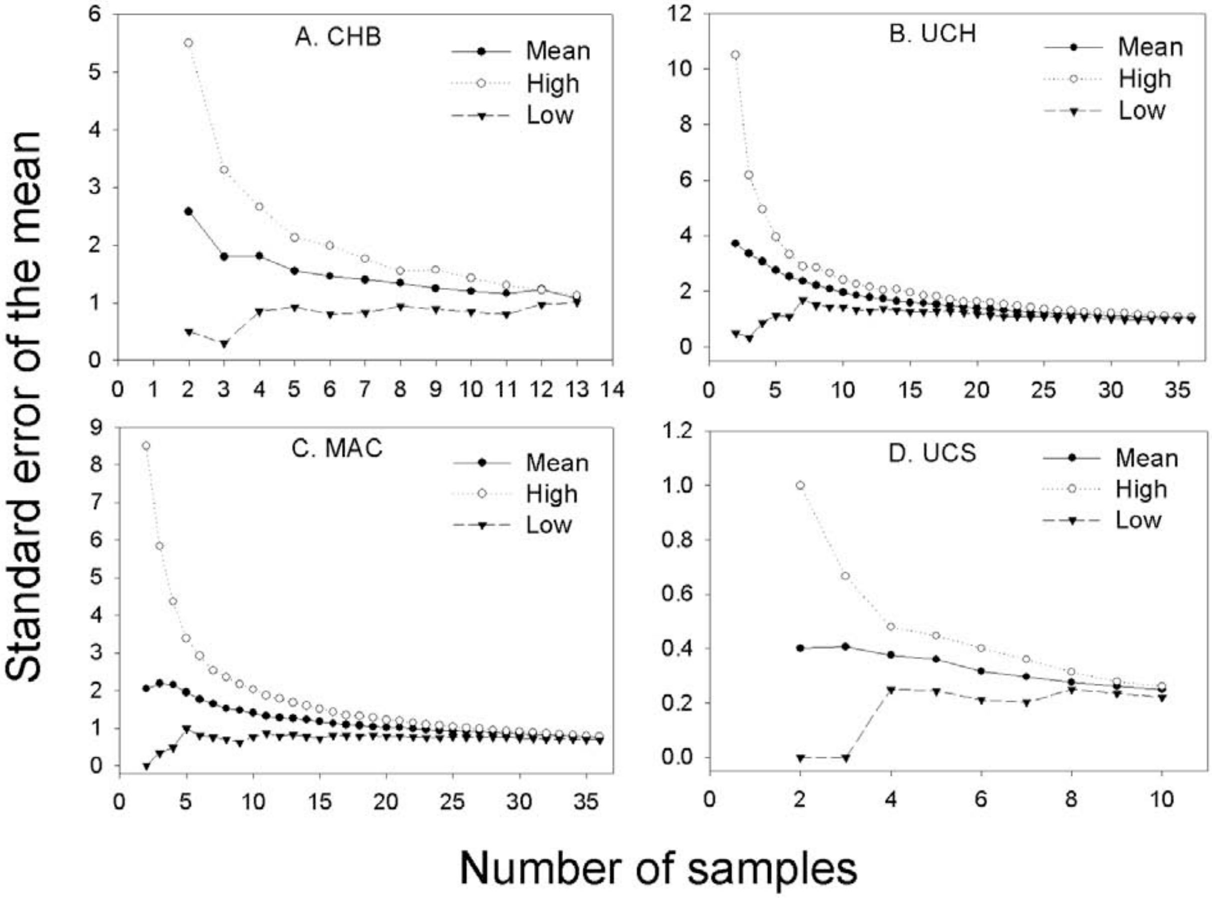

Figure 2. Sample size optimization for number of species per transect. Relationship between standard error of the mean (SEM) and sample size for habitat types. Monte Carlo simulation procedure for sample size optimization described by Bros and Cowell (1987). CHB = colonized hard bottom, UCH = uncolonized hard bottom, MAC = macroalgae, and UCS = unconsolidated sediment.

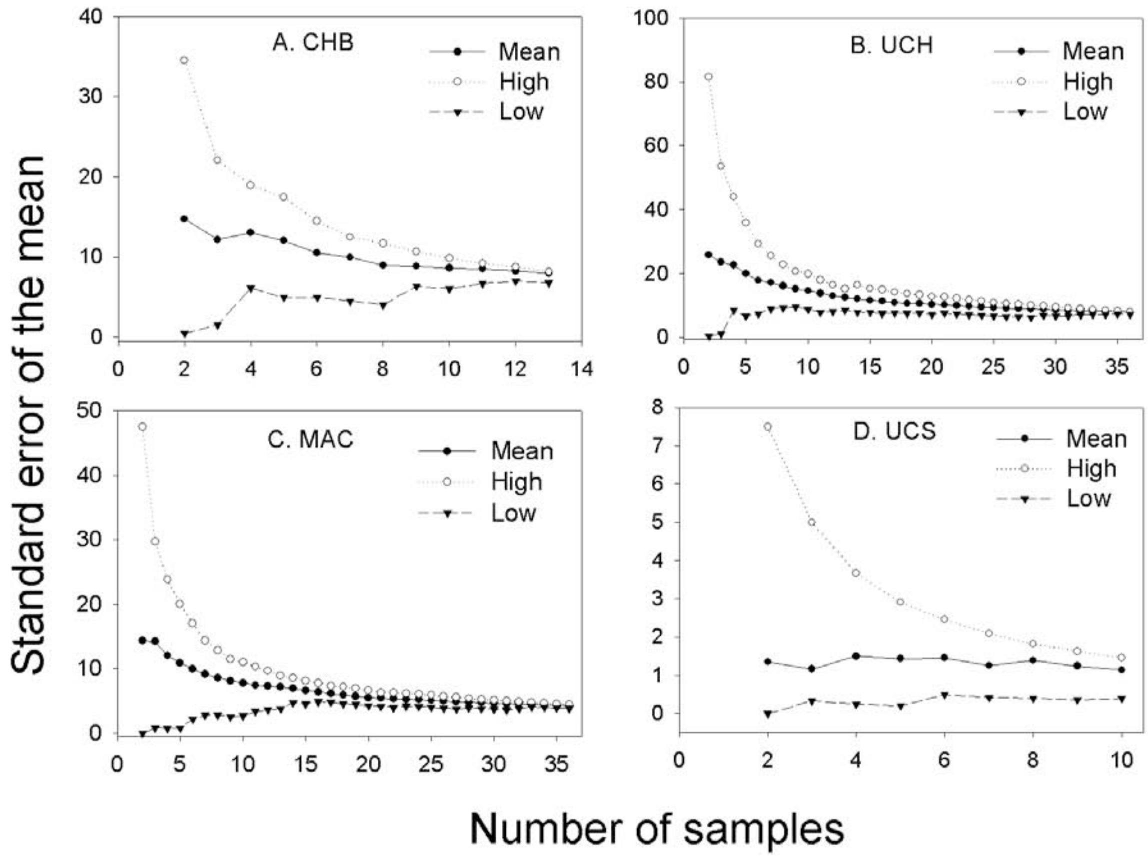

Figure 3. Sample size optimization for number of individuals per transect. Relationship between standard error of the mean (SEM) and sample size for habitat types. Monte Carlo simulation procedure for sample size optimization described by Bros and Cowell (1987). CHB = colonized hard bottom, UCH = uncolonized hard bottom, MAC = macroalgae, and UCS = unconsolidated sediment.

Benthic survey techniques
The Waikiki MLCD and surrounding benthic habitats were sampled using digital video transects to measure percent cover of different substrate types. Each transect was 25m in length and videotaped from a perpendicular angle at a height of 0.5m above the substrate. Total area sampled along each transect was $12.8m^2$. Image analysis was conducted using PointCount 99 software on 20 randomly selected non-overlapping video frames from each transect with 50 randomly selected points per frame. Percent cover was tabulated for coral (by species), macroinvertebrates, and other benthic substrate types (coralline algae, turf algae, macroalgae/*Halimeda* spp., and sand). Total mean percent coral cover by station, mean percent coral cover by species within a station, and species richness (number of species per transect) were used as dependent variables. Long post processing time (2 hours for 1 transect), however, and low taxonomic resolution of other substrate categories (e.g. macroalgae) necessitated changing methodology to *in-situ* visual quadrats.

Subsequent to data collection at Waikiki, coral species richness, percent coverage, and diversity were examined using the *in-situ* planar point intercept quadrat method (Reed 1980). Each 25m fish transect was stratified into 5 x 5m segments with quadrat placement randomly allocated within each segment. The quadrat grid was $1m^2$ in area and consisted of 1 inch PVC tubing fitted with nylon line spaced 10 centimeters apart to form a square grid with 81 intersections. A subset of 25 randomly selected intersections were marked and used for substrate identification. The rationale for the subset was that 25 points sufficiently represented the habitat with acceptable error and optimized sampling time (Brown, unpublished manuscript, Fig. 4). Each intersection was identified using substrate categories of sand, coralline algae, turf algae, macroalgae, *Halimeda spp*, and coral. Coral and macroinvertebrates were identified down to species using Veron (2000) and Hoover (2002) respectively. The macroinvertebrates category incorporated echinoderms and other large invertebrates (e.g. zooanthids, octocorals) that occupied significant portions of the substrate. Macroinvertebrates were also included in the results for comparative purposes, but the methodology limited conclusions about distribution and abundance for this group of organisms. Limitations of *in-situ* methodology precluded taxonomic resolution of algae down to the species level so algae were identified to genera using Littler and Littler (2003). Percent cover values for each substrate category and coral species were derived by dividing the number of occupied points by the total number of intersections (25) within each quadrat.

Rugosity methods
To measure reef rugosity or surface relief, a chain of small links (1.3 cm per link) was draped along the full length of the centerline of each transect (Risk 1972). Care was taken to ensure that the chain followed the contour of all natural fixed surfaces directly below the transect centerline. A ratio of distance along the reef surface contour to linear horizontal distance gave an index of spatial relief or rugosity.

Sample Design
A stratified random sampling design was employed (Fig. 5). Habitat polygons were attributed into four major habitat types (colonized hard bottom, uncolonized hard bottom, macroalgae, and sand). Within each major habitat type, sampling was further stratified by management regime (MLCD, FMA, and open access). All sampling locations were randomly generated in ArcView 3.2.

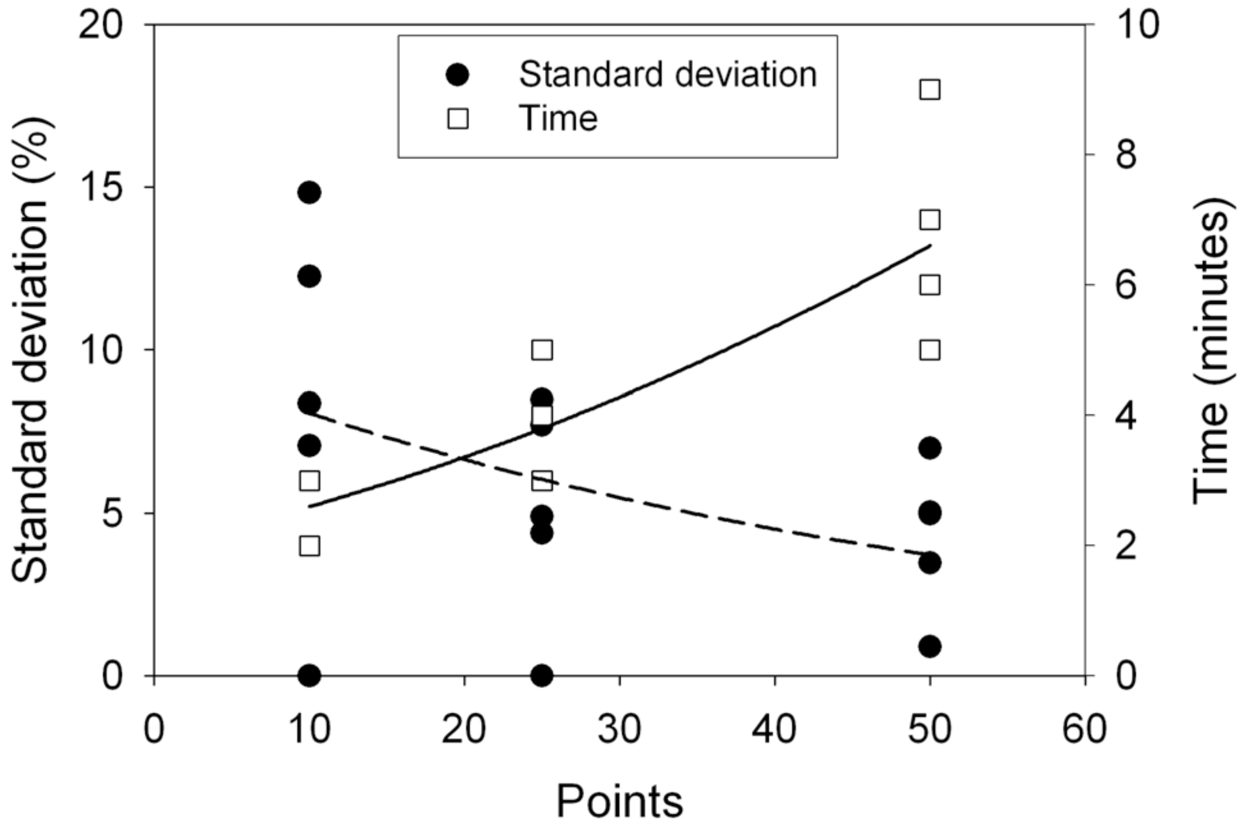

Figure 4. Standard deviation (left Y-axis) in percent and sampling time (right Y-axis) as a function of number of points per quadrat.

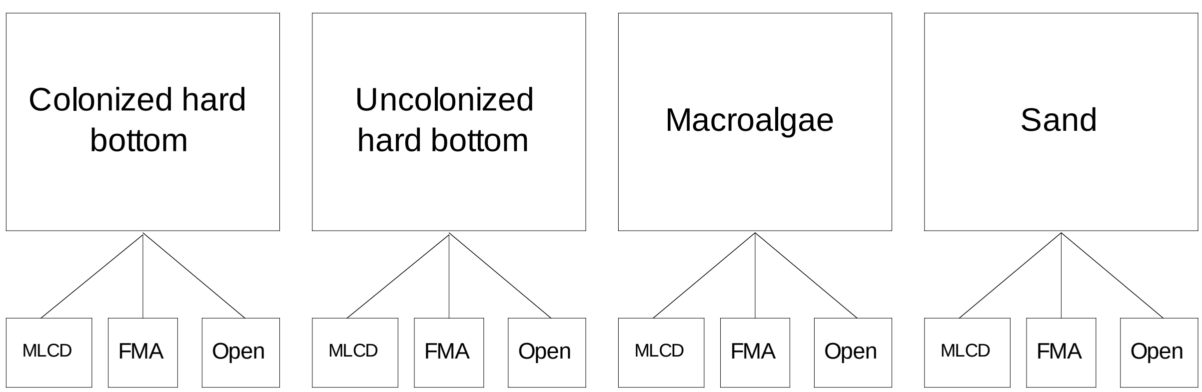

Figure 5. A stratified random sampling design was employed to assess MLCDs, FMAs, and areas open to fishing by major habitat types.

Data Analysis
A biogeographic assessment was conducted to define essential fish habitat and evaluate MPAs (Fig. 6). For fish assemblage characteristics, number of individuals and biomass were ln(x+1) transformed for statistical analysis. Numbers of individuals were converted to number/ha and biomass was converted to t/ha for comparisons with other studies throughout the state. Comparisons of fish species richness, biomass, and diversity among management strata were conducted using a Nested Analysis of Variance (ANOVA) using only the habitat types common to all management strata. Significant differences between pairs were examined using the Tukey-Kramer HSD (honestly significant difference) test for ANOVAs ($\alpha = 0.05$).

Species diversity was calculated from the Shannon-Weaver Diversity Index (Ludwig and Reynolds 1988): H'=S (pi ln pi), where pi is the proportion of all individuals counted that were of species i. An index of relative dominance (IRD) for each fish taxa was created by multiplying the percent frequency of occurrence of the taxa on each transect by the relative percent number of that taxa (Greenfield and Johnson 1990).

Non-metric Multi Dimensional Scaling (MDS) analysis was conducted to examine fish assemblage structure among habitats and management regimes. The data matrix consisted of mean fish biomass by species for each major habitat within each management strata at each overall location. A Bray-Curtis Similarity matrix was created from the ln(x+1) transformed mean fish biomass matrix prior to conducting the MDS.

The top ten benthic species/substrates, in terms of percent cover, were compiled for each site by management regime. Substrate cover within each site was statistically examined using a General Linear Model (GLM) two-way ANOVA with percent cover as the dependent variable and management regime (2 levels, Marine Life Conservation District and Open Access) and substrate type (6 levels, Coralline algae, Coral, Macroinvertebrates, Macroalgae, Sand/Bare Rock, and Turf algae) as factors. Percent substrate cover data were subjected to an arcsine-square root transformation prior to testing to meet the assumptions of normality and homogeneity of variances (Zar 1999). Each site was analyzed separately to focus on differences among substrate types across management regimes. Post-hoc multiple comparisons among substrate types used Tukey's unequal Honest Significant Differences (HSD) at $\alpha = 0.05$. Three sites (Kealakekua Bay, Old Kona Airport, and Waikiki) included a third management stratum (Fisheries Management Area) which was adjacent to the conservation district. In addition, a seventh substrate type of "Plant" was used in the Hanauma Bay and Kaneohe Bay analyses to account for the presence of *Halophila hawaiiensis.* Raw percent cover data were used for display purposes, but presentation of statistical results used the transformed data.

In the overall comparison, a GLM 2 way ANOVA was used to examine percent coral and macroalgae cover (dependent variables) among islands (4 levels: Oahu, Lanai, Maui, and Hawaii). Additional GLM 2 way ANOVA tests were conducted to examine percent coral and macroalgae cover (dependent variables) among sites (12 levels), and management regimes (3 levels: Marine Life Conservation District, Open Access, and Fisheries Management Area). Unconsolidated sediment habitats were excluded from the analysis because they were similar (i.e. all sand) across all of the factor levels. In addition, only coral and macroalgae were included in the analysis due to the importance of these functional substrate types.

Nonmetric Multidimensional Scaling (MDS) using PRIMER v5 (Clarke and Gorley 2001) was used to explore the relationship among colonized hardbottom benthic assemblages at the site level across islands and management regimes. In a separate MDS analysis, uncolonized hardbottom benthic assemblages were also examined at the site level across islands and management regimes. In both analyses, percent cover for the different taxa was averaged within each site and management regime. Distinctive groupings in the MDS plots were examined using the SIMPER procedure in PRIMER that listed taxa in decreasing order of importance in discriminating between benthic assemblages.

Presentation of benthic results was simplified to focus on the statistical analysis of the fish assemblage characteristics. Therefore, only mean values of benthic cover are reported in the tables with error estimates shown in the figures. In addition, ANOVA and multiple comparison tables are excluded but the results of the statistical analyses are graphically presented in the figures.

Fish size spectra were described for each management strata using least squares regression to relate log10-transformed biomass densities against body length in 5 cm size classes. Lengths were first standardized to the midpoint of the size distribution for each management strata in order to remove the correlation between slope and intercept (Dulvy et al. 2004; Graham et al. 2005). Estimates were restricted to fish ≥ 15-cm TL largely to eliminate the influence of recent recruitment on size distributions. Size spectra were compared among management strata using least squares Analysis of Covariance (ANCOVA). For both statistical procedures above, unplanned multiple comparisons were tested using Tukey's HSD test ($\alpha = 0.05$). Regression models of fish biomass ($\ln x + 1$) vs. habitat rugosity and herbivore biomass vs. macroalgae cover were also compared using ANCOVA.

Stepwise multiple regression analyses were conducted to assess the importance of various independent variables on fish assemblage characteristics (species richness, biomass, and diversity). Independent variables included percent cover of live coral, macroalgae, sand, turf algae, as well as rugosity, depth, and whether the transect was protected from fishing (MLCDs and Moku o Loe Refuge) or open to fishing (open areas and FMAs). Percent cover data were arcsin square root transformed prior to analyses. Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion was based on Mallow's Cp criterion for selecting a model. It is an alternative measure of total squared error defined as:

$$Cp=(SSEp/s2) - (N - 2p)$$

where s2 is the MSE for the full model and SSEp is the sum-of-squares error for a model with p variables and the intercept. If Cp is graphed with p, Mallows (1973) recommends choosing the model where Cp first approaches p.

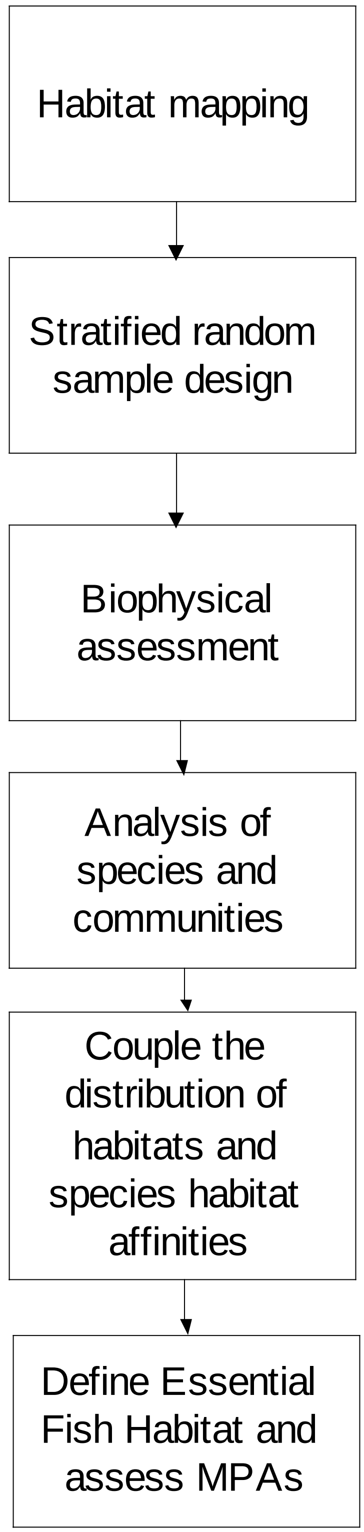

Figure 6. Biogeographic assessment to define essential fish habitat and evaluate MPAs.

RESULTS

Waikiki MLCD and adjacent area
The Waikiki study area extended from the Ala Wai Harbor to Black Point (ca. 6.5km) and included the Waikiki MLCD and Waikiki-Diamond Head FMA.

Sample allocation
A total of 99 samples were collected between January 20 and April 30, 2002 (Fig. 7; Table 3). The two levels of sampling stratification included major habitat types (CHB, MAC, UCH, and sand) and fisheries management regime (open access, FMA, and MLCD). The Waikiki-Diamond Head FMA is open to limited fishing during even-numbered years and closed to all fishing during odd-numbered years. Sampling was conducted during the open fishing period. Only macroalgae and uncolonized hardbottom were sampled in the FMA and MLCD strata. Sand and colonized hardbottom were not present at the one-acre minimum mapping unit within the MLCD and the colonized hardbottom habitat within the FMA was small and difficult to sample owing to its shallow nearshore location.

Table 3. Sample allocation for Waikiki study area.

Habitat	Open	FMA	MLCD	Total
Colonized hardbottom	14	-	-	14
Macroalgae	17	9	11	37
Uncolonized hardbottom	16	11	10	37
Sand	11	-	-	11
Total	58	20	21	99

Large-scale benthic cover
Benthic coverage for the Waikiki MLCD was derived from the NOAA benthic habitat maps, with macroalgae (44%) and uncolonized hardbottom (42%) comprising more than 86% of the total benthic habitat in the MLCD. Sand accounted for an additional 13% of the benthic cover in the MLCD (Fig. 7; Table 4).

Table 4. Benthic cover for the Waikiki MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Artificial	Manmade feature	561	0.18
Macroalgae	50%-<90%	138409	44.10
Sand		41950	13.37
Uncolonized Hardbottom	Uncolonized pavement	132924	42.35
Grand total		313844	100.00

Small-scale benthic cover of substrate types within the management regimes.
The most abundant substrate type in all 3 strata was turf algae, which averaged 65% to 69 % cover (Table 5; Fig. 8). Sand was also prevalent in the Marine Life Conservation District (MLCD - 21%) and the open access areas (25%), but only occupied 5% of the substrate in the Fisheries Management Area (FMA). In contrast, macroalgae was most abundant in the FMA (25%) compared to the MLCD (11%) and the open access area (8%). Unfortunately, the low resolution of the video images limited macroalgae identification but *in-situ* observations identified two predominant species, *Acanthopora spicifera* and *Gracilaria salicornis.* These 3 substrate types comprised between 97% and 99% of the benthic cover within each of the management strata compared to coral cover which was less than 3%. *Porites lobata* and *Pocillopora meandrina* were the primary coral species found in the MLCD and the FMA. Only the open access area had transects with coral cover exceeding 10%. The remaining macorinvertebrates and coralline algae were less than 1% of the benthic cover.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types (Table 5; Fig. 8). This result indicated that comparing fish assemblages across the management strata was appropriate at the major substrate types.

Fish assemblage characteristics among habitat types and management regimes
Fish assemblage characteristics (species richness, biomass, and diversity) were generally higher in the MLCD, compared to the FMA and open area (Fig. 9, 10, and 11). The colonized hardbottom open area had the greatest number of species, followed by uncolonized hardbottom, macroalgae, and sand, respectively (Fig. 12). Biomass was highest in the uncolonized hardbottom habitat followed by colonized hardbottom habitat and macroalgae (Fig. 13). Trends in diversity among habitats were similar to those observed for species richness (Fig. 14). Few fishes were observed in the sand habitat.

In the two habitat types (macroalgae and uncolonized hard bottom) common to all three management regimes, fish assemblage characteristics were highest within the MLCD, followed by the FMA and open access areas, respectively (Table 6A, 6B, and 6C). Biomass was significantly greater ($p<0.05$) in the MLCD compared to the FMA, while species richness and diversity were similar between these two regimes ($p>0.05$). Species richness and diversity were significantly lower in the open area ($p<0.05$) compared with the FMA and MLCD, while biomass between the open area and the FMA were not significantly different ($p>0.05$).

Fish trophic structure among habitat types and fisheries management regimes
Herbivores were the dominant trophic guild by weight; accounting for over 67% of the total fish biomass over all habitat types. Secondary consumers comprised an additional 32% of biomass (Fig. 15). Few apex predators were observed and accounted for only 1% of the total fish biomass observed over the study area. Herbivores were most abundant in the uncolonized habitat in the MLCD, followed by the MLCD macroalgae habitat and open access colonized hardbottom. The highest biomass of secondary consumers was observed in the open access colonized hardbottom, uncolonized FMA, and uncolonized MLCD habitats.

Table 5. Top 10 benthic taxa/substrate types by percent cover within the Waikiki Marine Life Conservation District (MLCD), the open access area (Open) outside the MLCD, and inside the adjacent Fisheries Management Area (FMA). Note that the MLCD and the FMA only documented 7 and 6 substrate types respectively.

Marine Life Conservation District			Open Access			Fisheries Management Area		
Substrate Type	Taxon	%	Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		67.2	Turf algae		65.1	Turf algae		69.1
Sand		21.2	Sand		24.6	Macroalgae		25.2
Macroalgae		10.6	Macroalgae		7.9	Sand		4.6
Coral	*Porites lobata*	0.6	Coral	*Pocillopora meandrina*	1.0	Coral	*Pocillopora meandrina*	1.0
Coral	*Pocillopora meandrina*	0.4	Coral	*Porites lobata*	0.9	Macroinvertebrate	*Echinometra mathaei*	0.1
Coral	*Montipora patula*	0.0	Coralline algae		0.2	Coral	*Porites lobata*	0.1
Macroinvertebrate	*Holothuriidae*	0.0	Coral	*Montipora patula*	0.1			
			Non-coral (Tape)		0.1			
			Macroinvertebrate	*Diadema paucispinum*	0.0			
			Macroinvertebrate	*Echinometra mathaei*	0.0			

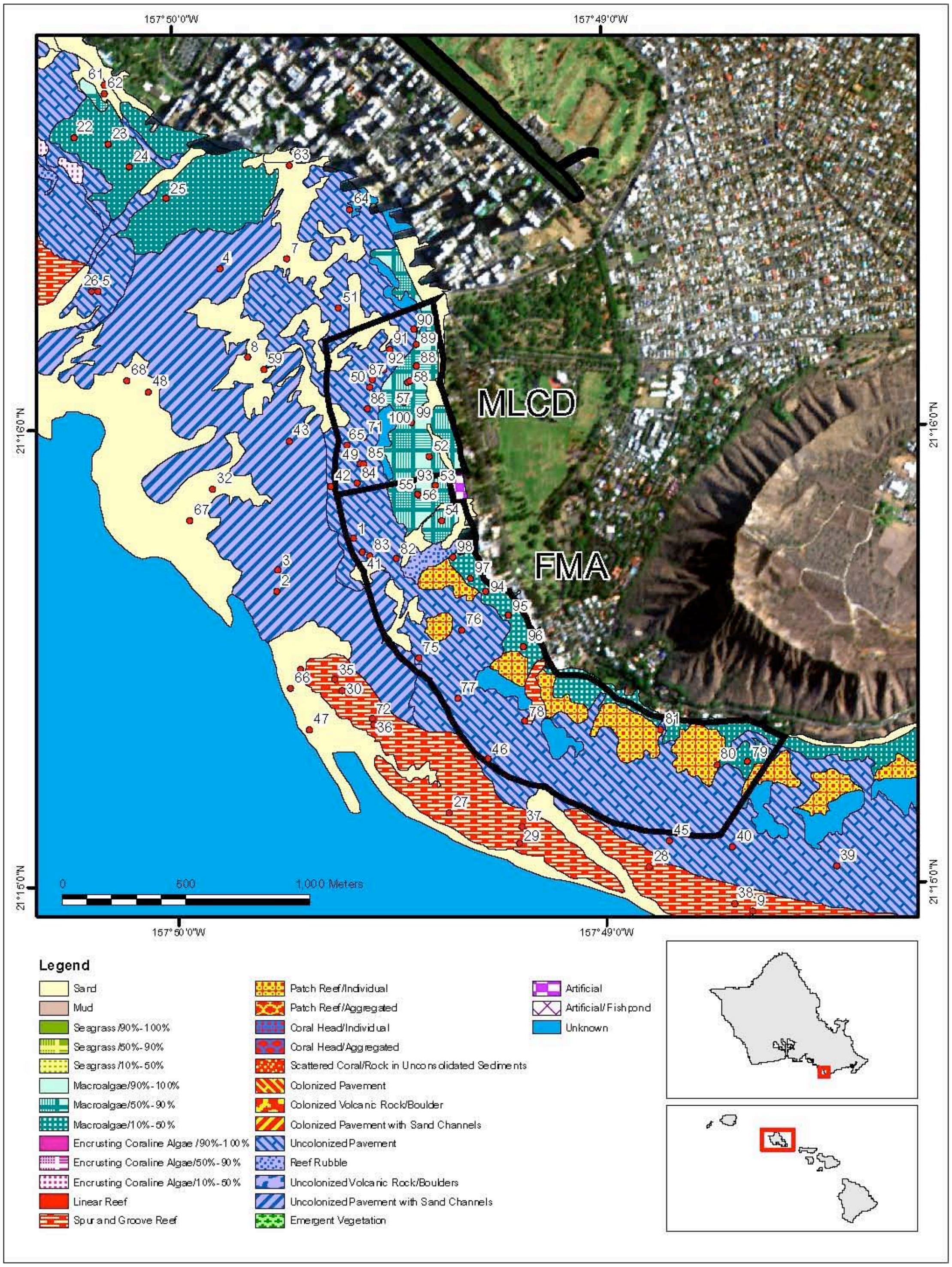

Figure 7. Sampling locations and benthic habitats for the Waikiki study area including the Waikiki MLCD and Waikiki-Diamond Head FMA.

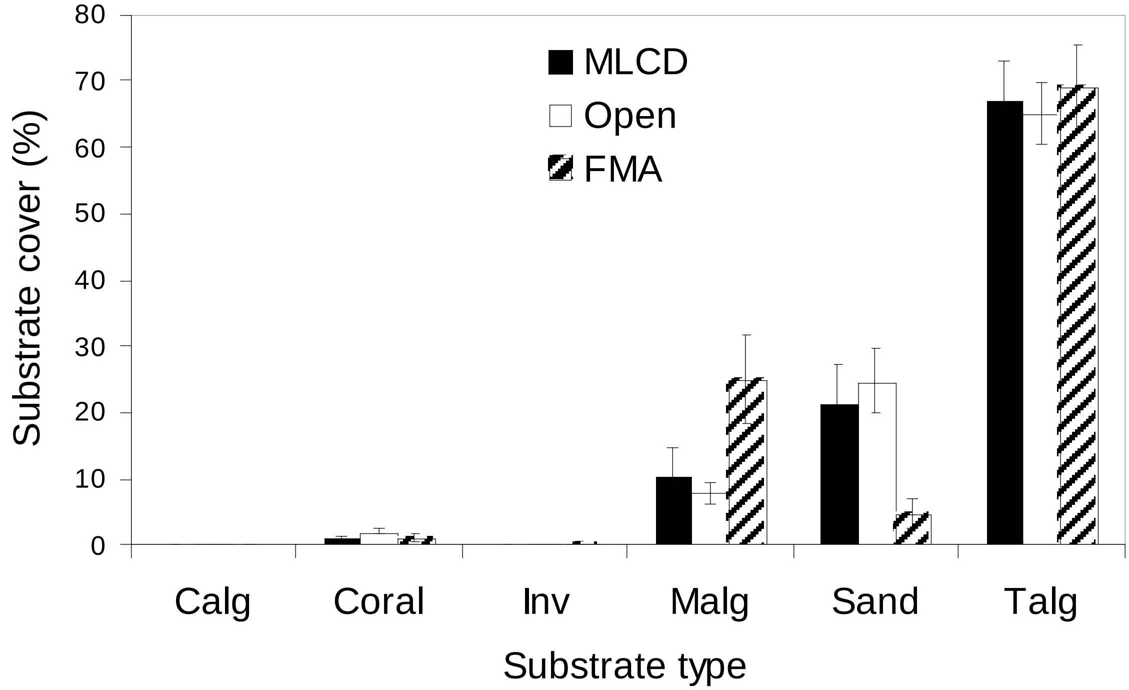

Figure 8. Mean percent cover of substrate types within the Waikiki Marine Life Conservation District (MLCD), open to all fishing (Open), and inside the adjacent Fisheries Management Area (FMA). Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

<u>Species composition by management regime</u>

Within the MLCD, resource species such as bluespine unicornfish (*kala*, *Naso unicornis*), whitebar surgeonfish (*maikoiki*, *Acanthurus leucopareius*), and ringtail surgeonfish (*pualu*, *Acanthurus blochii*) accounted for much of the fish biomass observed (Table 7). In comparison, much of the biomass in areas open to fishing consisted of low value species such as brown surgeonfish (*maiii*, *Acanthurus nigrofuscus*), reef triggerfish (humuhumunukunukuapuaa, *Rhinecanthus rectangulus*), lei triggerfish (*humuhumulei*, *Sufflamen burse*), and saddle wrasse (*hinalea lauwili*, *Thalassoma duperrey*) (Table 9). The FMA was somewhat intermediate in its abundance, with resource species such as bluespine unicornfish (*kala*) and convict tang (*manini*, *Acanthurus triostegus*) providing important contributions to total fish biomass (Table 8).

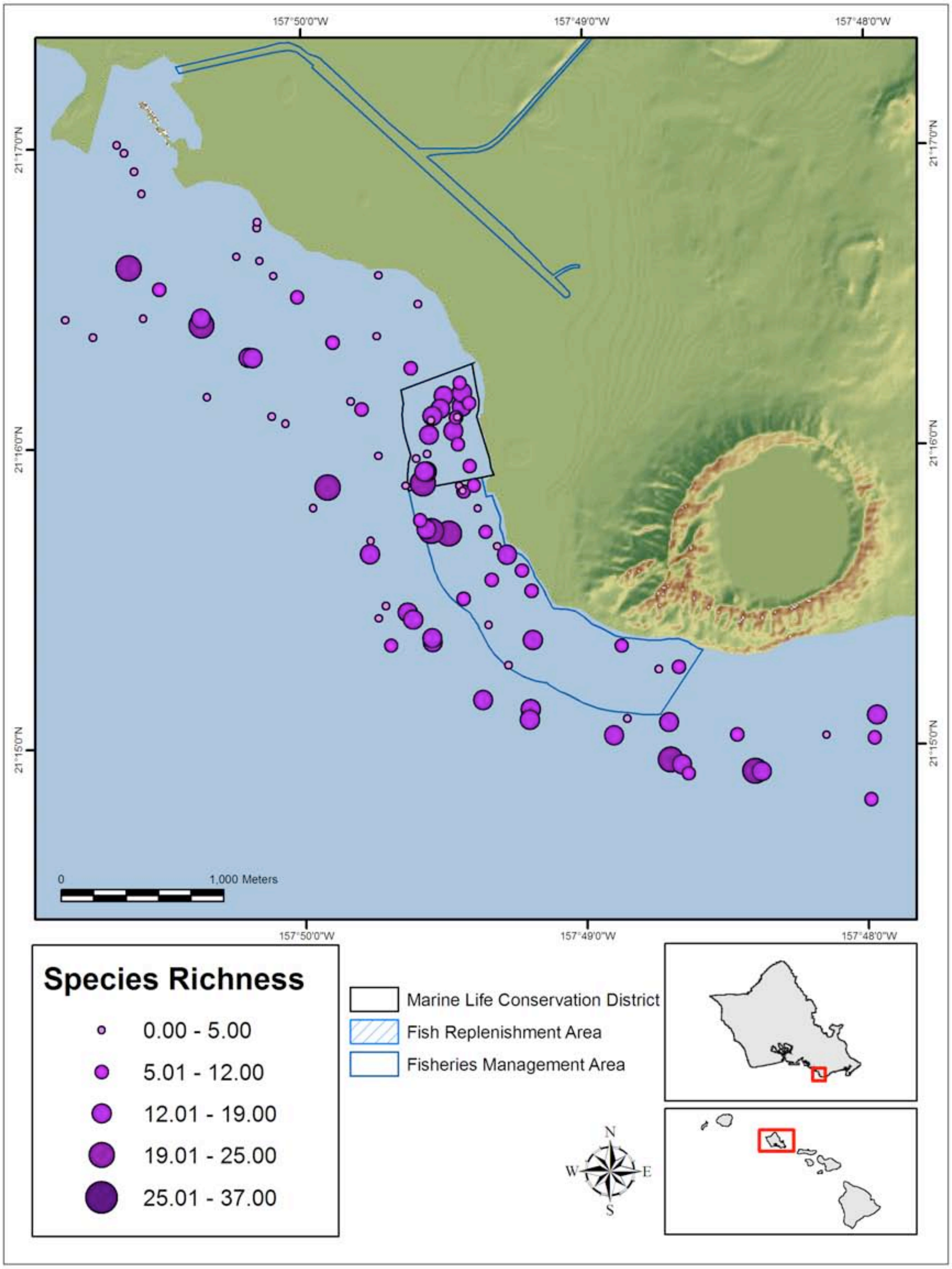

Figure 9. Species richness by individual transects (N=99) for Waikiki study area, including Waikiki MLCD and Waikiki-Diamond Head FMA. Classification based on quantiles.

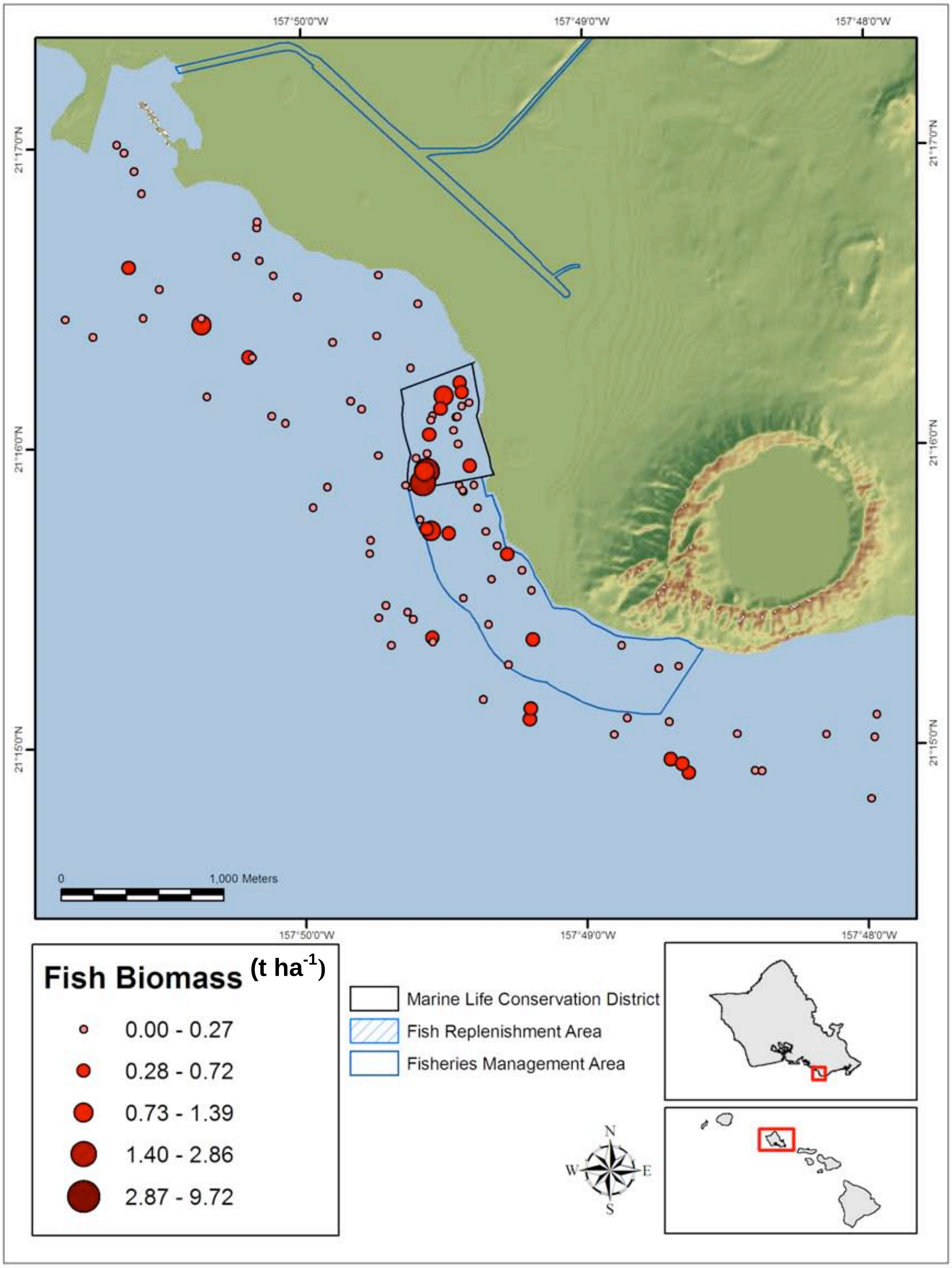

Figure 10. Fish biomass (t ha^{-1}) by individual transects (N=99) for Waikiki study area, including Waikiki MLCD and Waikiki-Diamond Head FMA. Classification based on quantiles.

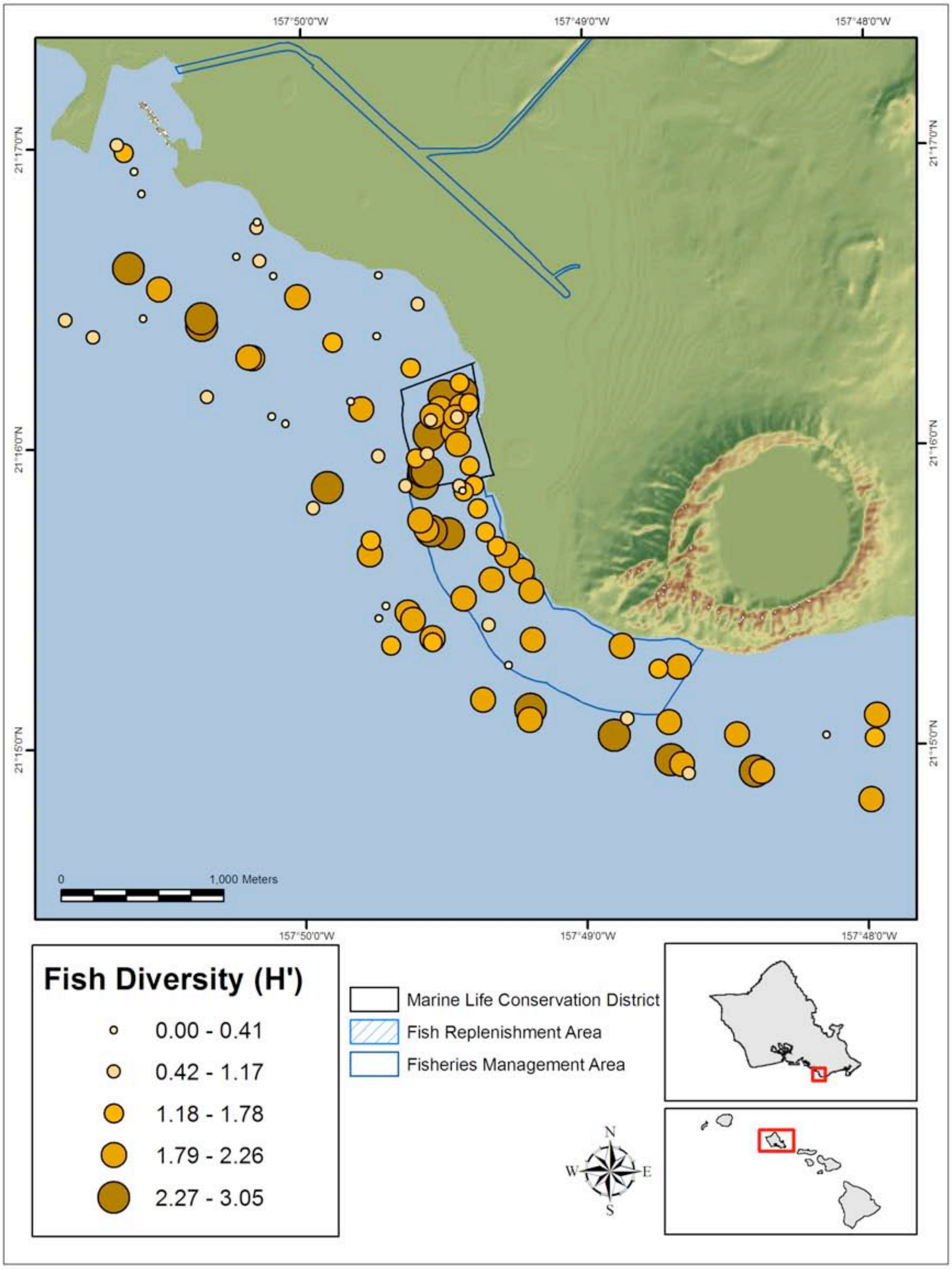

Figure 11. Fish diversity (H') by individual transects (N=99) for Waikiki study area, including Waikiki MLCD and Waikiki-Diamond Head FMA. Classification based on quantiles.

Table 6A. Comparison of fish species richness among management regimes and habitat types for Waikiki study area, including Waikiki MLCD and Waikiki-Diamond Head FMA. Results of nested ANOVA with major habitat types common to all management regimes nested within management regime (N = 74). Management regimes: MLCD ([M]), FMA ([F]), and Open (completely open to fishing ([O])). Habitat strata: <10% live coral hard bottom (UCH), and macroalgae (MAC). Unplanned multiple comparisons among management strata and habitat$_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different ($\alpha = 0.05$)

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	199.6	7.05	<0.001	
Management	2	90.5	3.20	0.047	MLCD = FMA > Open
Habitat$_{[management]}$	3	266.5	9.41	<0.001	
Error	68	28.3			
Habitat$_{[management]}$ -					UCH$_{[M]}$ UCH$_{[F]}$ UCH$_{[O]}$ MAC$_{[M]}$ MAC$_{[F]}$ MAC$_{[O]}$

Table 6B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for Waikiki study area, including Waikiki MLCD and Waikiki-Diamond Head FMA. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	0.19	5.10	0.0005	
Management	2	0.28	7.25	0.0140	MLCD > FMA = Open
Habitat$_{[management]}$	3	0.15	3.81	0.0313	
Error	68	0.04			
Habitat$_{[management]}$ -					UCH$_{[M]}$ UCH$_{[F]}$ MAC$_{[M]}$ UCH$_{[O]}$ MAC$_{[F]}$ MAC$_{[O]}$

Table 6C. Comparison of fish species diversity (H') among management regimes and habitat types for Waikiki study area, including Waikiki MLCD and Waikiki-Diamond Head FMA.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	2.79	8.15	<0.001	
Management	2	2.54	7.42	0.001	MLCD = FMA > Open
Habitat$_{[management]}$	3	2.84	8.31	<0.001	
Error	68	0.34			
Habitat$_{[management]}$ -					UCH$_{[M]}$ UCH$_{[F]}$ UCH$_{[O]}$ MAC$_{[M]}$ MAC$_{[F]}$ MAC$_{[O]}$

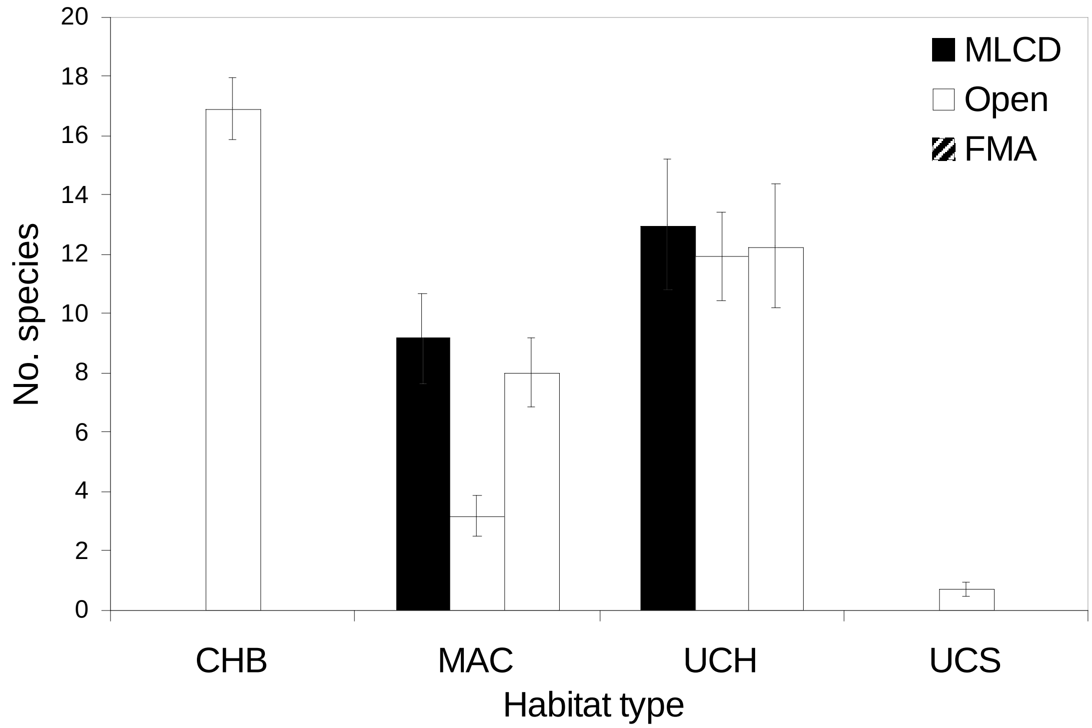

Figure 12. Mean number of species per transect (125 m^2) by habitat type and management regime for the Waikiki study area. Error bars are standard error of the mean.

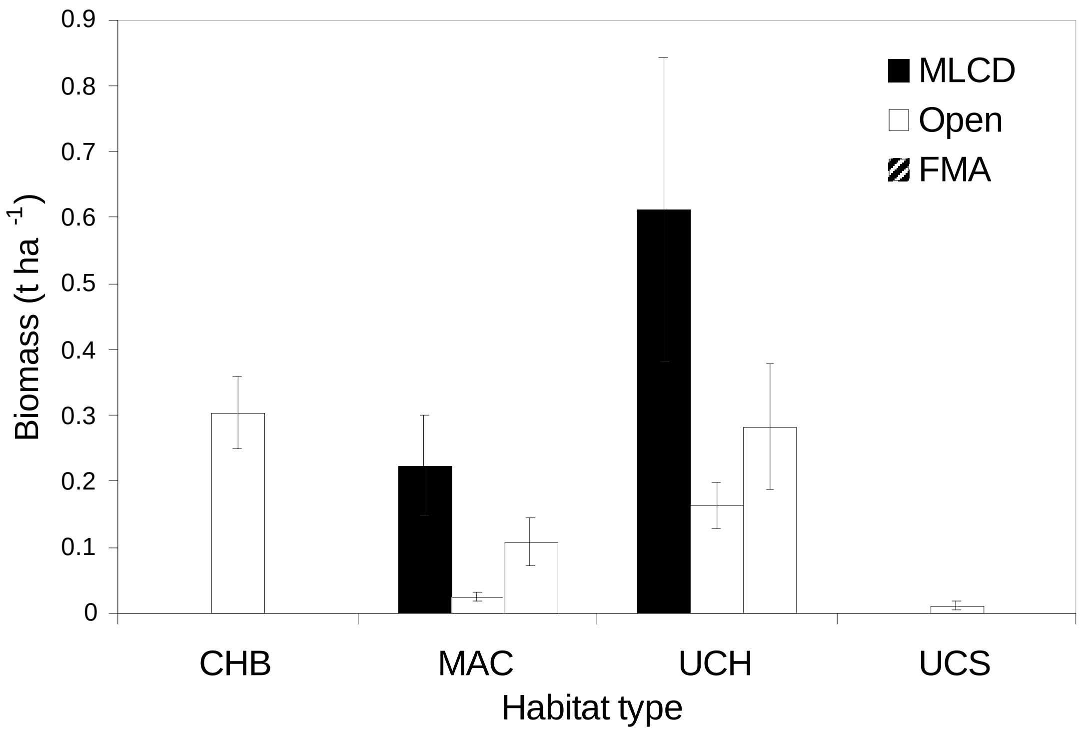

Figure 13. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the Waikiki study area. Error bars are standard error of the mean.

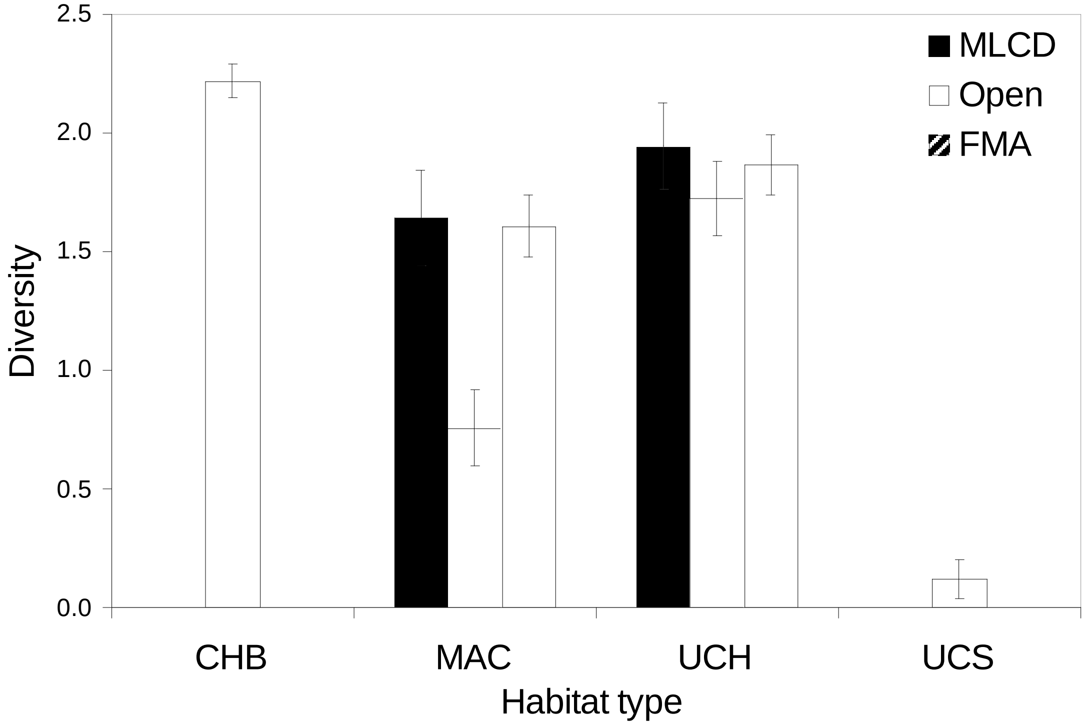

Figure 14. Mean diversity (H’) per transect (125 m^2) by habitat type and management regime for the Waikiki study area. Error bars are standard error of the mean.

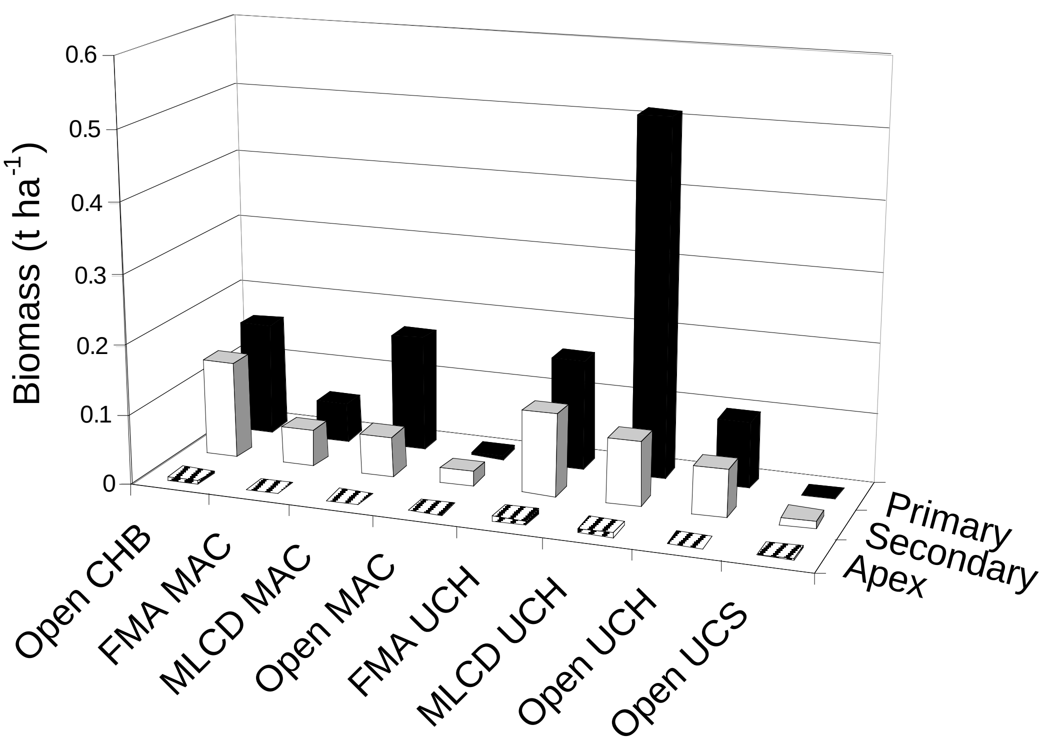

Figure 15. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the Waikiki study area.

Table 7. Top ten species in the Waikiki MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.50	0.063	66.67	12.44	15.50	1033.66
Naso unicornis	Bluespine Unicornfish	*kala*	0.16	0.061	57.14	4.11	15.02	858.23
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.18	0.048	28.57	4.40	11.75	335.72
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.73	0.013	95.24	18.28	3.23	307.37
Acanthurus triostegus	Convict Tang	*manini*	0.32	0.023	42.86	8.13	5.55	237.99
Rhinecanthus rectangulus	Reef Triggerfish	*humuhumunukunuk uapuaa*	0.08	0.012	66.67	2.11	2.93	195.45
Abudefduf abdominalis	Sargent Major	*mamo*	0.27	0.017	33.33	6.70	4.10	136.60
Stethojulis balteata	Belted Wrasse	*omaka*	0.30	0.005	80.95	7.46	1.25	101.57
Acanthurus blochii	Ringtail Surgeonfish	*pualu*	0.12	0.022	19.05	2.97	5.28	100.50
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.06	0.014	23.81	1.53	3.37	80.20

Table 8. Top ten species in the Waikiki-Diamond Head FMA, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.91	0.019	95.00	25.03	9.07	861.76
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.36	0.027	60.00	9.92	12.99	779.13
Stethojulis balteata	Belted Wrasse	*omaka*	0.60	0.008	100.00	16.43	4.06	405.68
Rhinecanthus rectangulus	Reef Triggerfish	*humuhumunukunuk uapuaa*	0.08	0.011	60.00	2.32	5.60	335.79
Acanthurus triostegus	Convict Tang	*manini*	0.21	0.013	40.00	5.73	6.32	252.94
Abudefduf abdominalis	Sargent Major	*mamo*	0.24	0.016	25.00	6.73	7.82	195.39
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.04	0.012	30.00	1.21	5.80	173.99
Naso unicornis	Bluespine Unicornfish	*kala*	0.05	0.016	15.00	1.32	7.76	116.41
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.06	0.006	30.00	1.76	3.13	93.93
Parupeneus multifasciatus	Manybar Goatfish	*moano*	0.05	0.004	35.00	1.32	1.99	69.56

Table 9. Top ten species in the Waikiki open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.45	0.018	37.93	14.00	14.11	535.39
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.49	0.009	50.00	15.30	7.01	350.27
Rhinecanthus rectangulus	Reef Triggerfish	*humuhumunukunukuapuaa*	0.07	0.009	44.83	2.30	6.93	310.45
Parupeneus multifasciatus	Manybar Goatfish	*moano*	0.22	0.005	50.00	7.07	4.15	207.48
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.08	0.009	31.03	2.60	6.65	206.35
Stethojulis balteata	Belted Wrasse	*omaka*	0.17	0.002	55.17	5.37	1.71	94.14
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.05	0.007	15.52	1.69	5.85	90.71
Melichthys niger	Black Durgon	*humuhumueele*	0.05	0.011	8.62	1.60	8.74	75.38
Acanthurus triostegus	Convict Tang	*manini*	0.10	0.008	10.34	3.29	6.31	65.30
Scarus psittacus	Palenose Parrotfish	*uhu*	0.10	0.004	17.24	3.16	3.25	56.12

Hanauma Bay MLCD and southeast Oahu

The south shore Oahu study area extended from Wailupe Peninsula to Sand Beach (ca. 9.1km) and included the Hanauma Bay MLCD.

Sample allocation

A total of 80 samples were collected between 4 and 25 May 2004 (Fig. 16A and 16B; Table 10). The two levels of sampling stratification included major habitat types (CHB, MAC, UCH, and sand) and fisheries management regime (open access and MLCD). Macroalgae habitat was not present at the one-acre minimum mapping unit within the MLCD.

Table 10. Sample allocation for south shore Oahu study area.

Habitat	MLCD	Open	Total
Colonized hardbottom	12	11	23
Macroalgae		11	11
Uncolonized hardbottom	10	15	25
Sand	11	10	21
Total	33	47	80

Large-scale benthic cover

Benthic coverage for the Hanauma MLCD was derived from the NOAA benthic habitat maps with sand accounting for 31% of the total habitat within the MLCD, followed by colonized pavement (25%), linear reef (12%), and uncolonized pavement (11%) (Table 11).

Table 11. Benthic cover for the Hanauma Bay MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized hardbottom	Aggregated coral	17185	4.22
	Colonized pavement	101107	24.80
	Colonized volcanic rock/boulder	31424	7.71
	Individual patch reef	7234	1.77
	Linear reef	47403	11.63
Sand		124422	30.52
Uncolonized hardbottom	Uncolonized pavement	43750	10.73
	Uncolonized volcanic rock/boulder	35150	8.62
Grand total		407676	100.00

Small-scale benthic cover of substrate types within the management regimes.

The most abundant substrate type was turf algae, which averaged 39% cover in the MLCD and 42 % cover in the open access area (Table 12; Fig. 17). Sand was also abundant in the Marine MLCD (37%) and the open access areas (30%). Macroalgae in the open access area covered 17% of the substrate which was attributed to the abundance of 3 genera, *Avrainvillea sp.* (5%), *Acanthophora sp.* (5%), and *Sprydia sp.* (1%) (Table 12). In contrast, total macroalgal cover in Hanauma Bay was <2% and composed primarily of *Melanamansia sp.* (1%). Total coral cover was 14% in the MLCD and 5% in the open area. *Porites lobata* (7%) and *Montipora patula* (3%) were the primary coral species in the MLCD compared to *Porites lobata* (2%) and *Pocillopora meandrina* (1%) in the open access areas. Cover of coralline algae was similar between the MLCD (8%) and open area (6%). The remaining macorinvertebrates were less than 1% of the benthic cover although *Palythoa caesia* occupied 0.5% of the substrate. Finally, several transects in the open access area documented low levels of *Halophila hawaiiensis* (0.1%) in the sand habitat.

Different management regimes had statistically similar levels of percent cover for each of the 7 substrate types even though cover of macroalgae and coral were quite different between the MLCD and the open areas (Fig. 17). This result indicated that comparing fish assemblages across the management strata was appropriate at the level of major subtrate types.

Fish assemblage characteristics among habitat types and between management regimes

Fish assemblage characteristics showed dramatic differences between the Hanauma Bay MLCD and adjacent areas (Fig. 18, 19, and 20). Among habitat types common to both management regimes, species richness, biomass, and diversity were all significantly higher in the MLCD (Table 13A, 13B, and 13C). Colonized hardbottom, followed by uncolonized hardbottom within the MLCD had the highest values for all assemblage characteristics (Fig. 21, 22, and 23). Biomass in the sand habitat within the MLCD was more than two times higher than uncolonized habitat in the open area.

Fish trophic structure between management regimes and among habitats

Primary consumers were seven times more abundant in the MLCD compared with the open area and were most abundant in the colonized hardbottom habitat (Fig. 24). Secondary consumers were 3.5 times more abundant by weight in the MLCD compared to the open area. The sand habitat within the MLCD harbored a substantial amount of secondary consumers, primarily goatfishes. Although apex predators comprised only 3% of the biomass in the MLCD, they were more than 68 times more abundant, by weight, compared to the open area.

Species composition by management regime

A number of important resource species were observed in MLCD, including the palenose parrotfish (*uhu, Scarus psittacus*), convict tang (*manini*), yellowstripe goatfish (*weke ula*, *Mulloidichthys vanicolensis*), orangespine unicornfish (*umaumalei*, *Naso lituratus*), and goldring surgeonfish (*kole*, *Ctenochaetus strigosus*) (Table 14). These five species accounted for 35% of the biomass in the MLCD. In contrast, the open area consisted of many small wrasses and other less desirable species (Table 15).

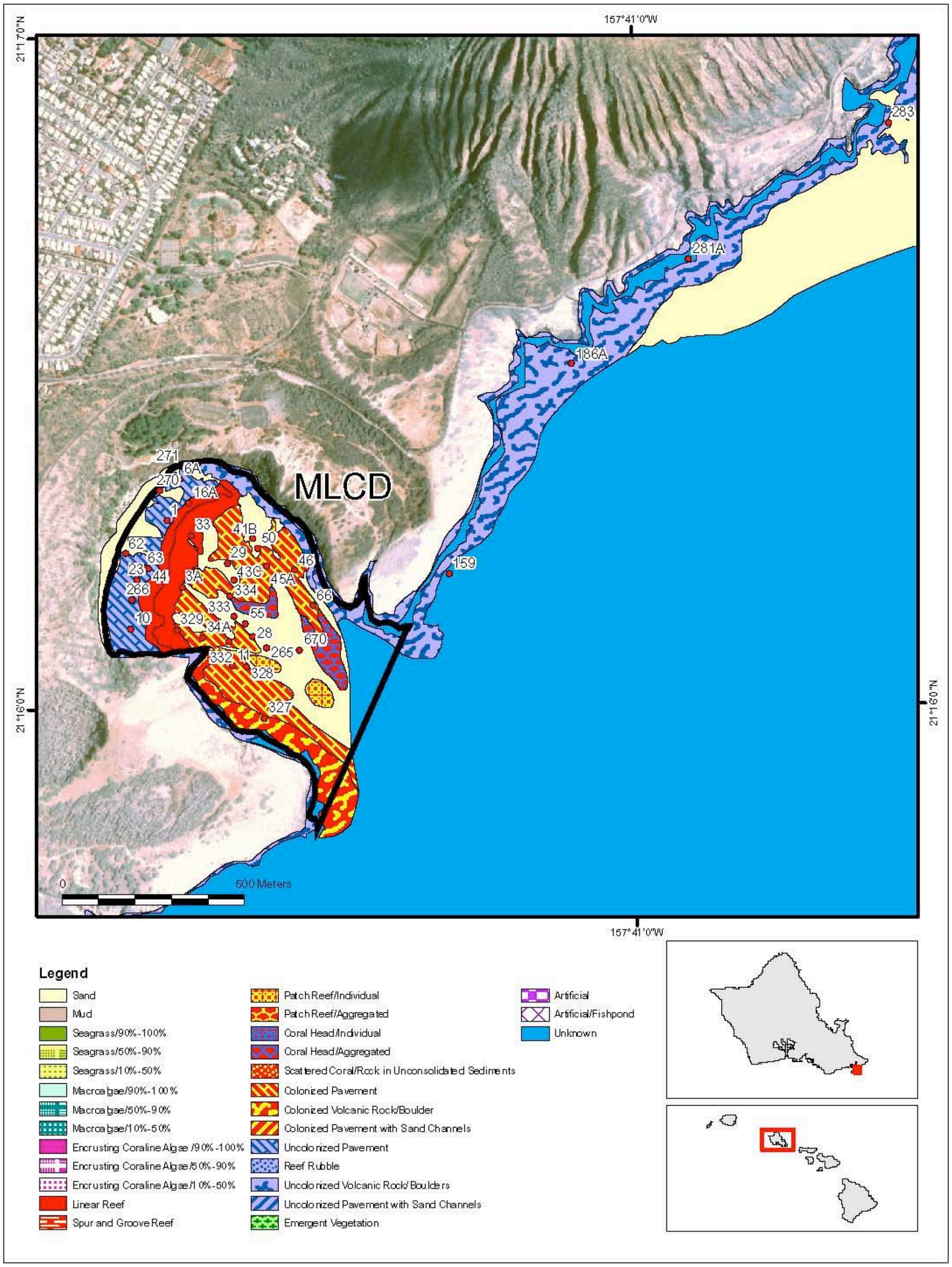

Figure 16A. Sampling locations and benthic habitats for the Hanauma Bay MLCD and adjacent areas.

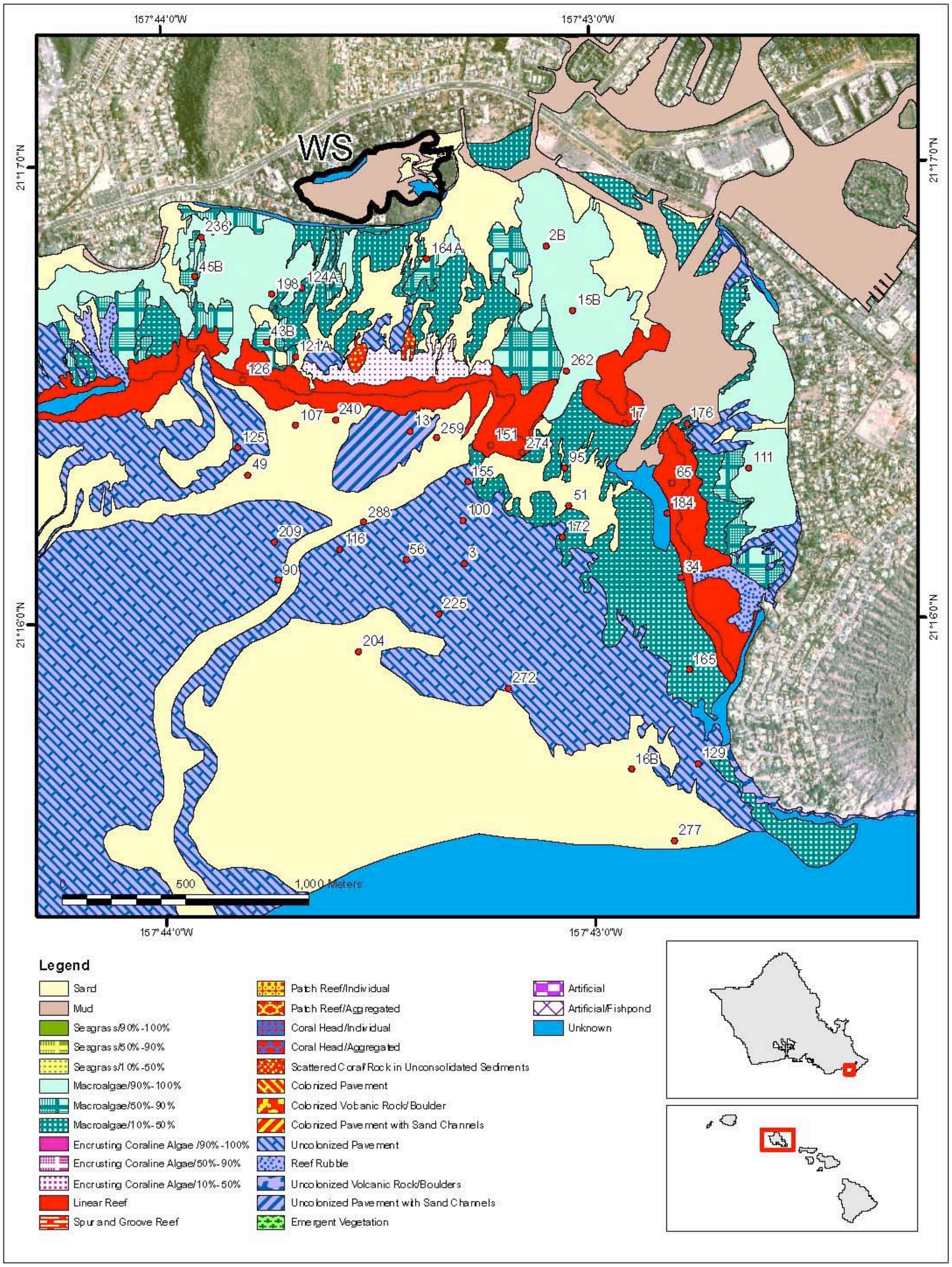

Figure 16B. Sampling locations and benthic habitats for the Hawaii Kai study area.

Table 12. Top 10 benthic taxa/substrate types by percent cover within the Hanauma Bay Marine Life Conservation District (MLCD) and the open access area (Open) outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		38.9	Turf algae		42.0
Sand		36.5	Sand		30.2
Coralline algae		7.6	Coralline algae		5.6
Coral	*Porites lobata*	7.3	Macroalgae	*Avrainvillea sp.*	5.2
Coral	*Montipora patula*	3.4	Macroalgae	*Acanthophora sp.*	5.1
Coral	*Montipora capitata*	1.2	Coral	*Porites lobata*	2.1
Macroalgae	*Melanamansia sp.*	1.1	Macroalgae	*Spyridia sp.*	1.4
Coral	*Pocillopora meandrina*	0.5	Coral	*Pocillopora meandrina*	1.1
Macroinvertebrate	*Palythoa caesia*	0.5	Coral	*Montipora patula*	0.7
Coral	*Porites compressa*	0.5	Macroalgae	*Codium sp.*	0.6

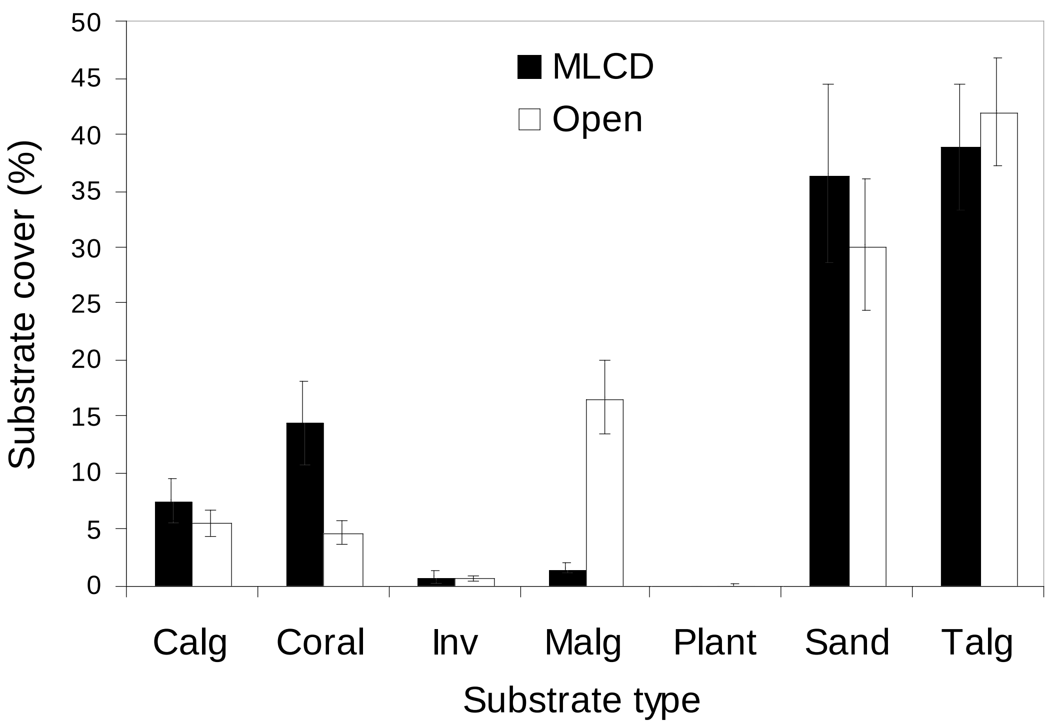

Figure 17. Mean percent cover of substrate types within the Hanauma Bay Marine Life Conservation District (MLCD) and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

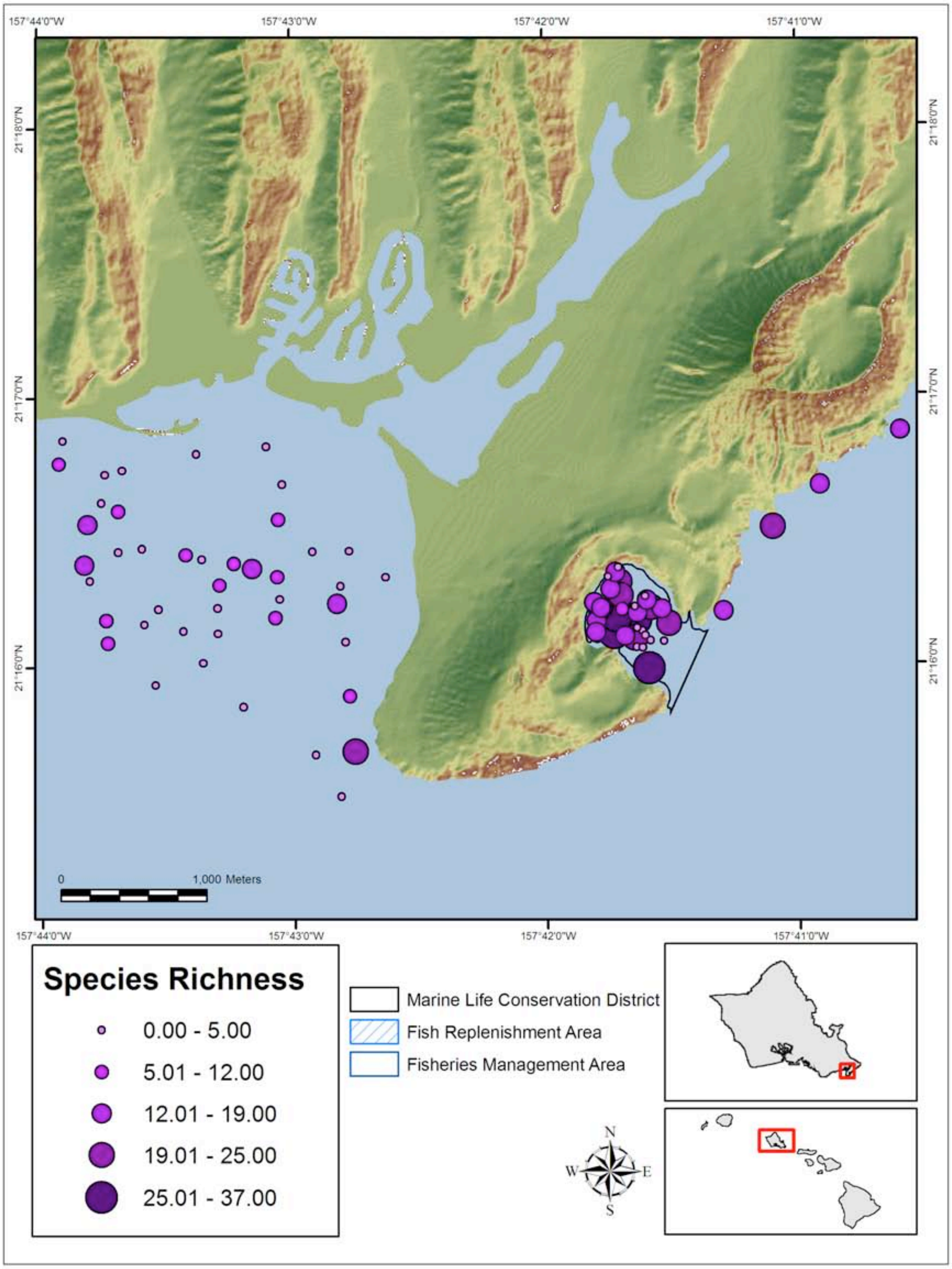

Figure 18. Species richness by individual transects (N=80) for southeast Oahu study area including Hanauma Bay MLCD. Classification based on quantiles.

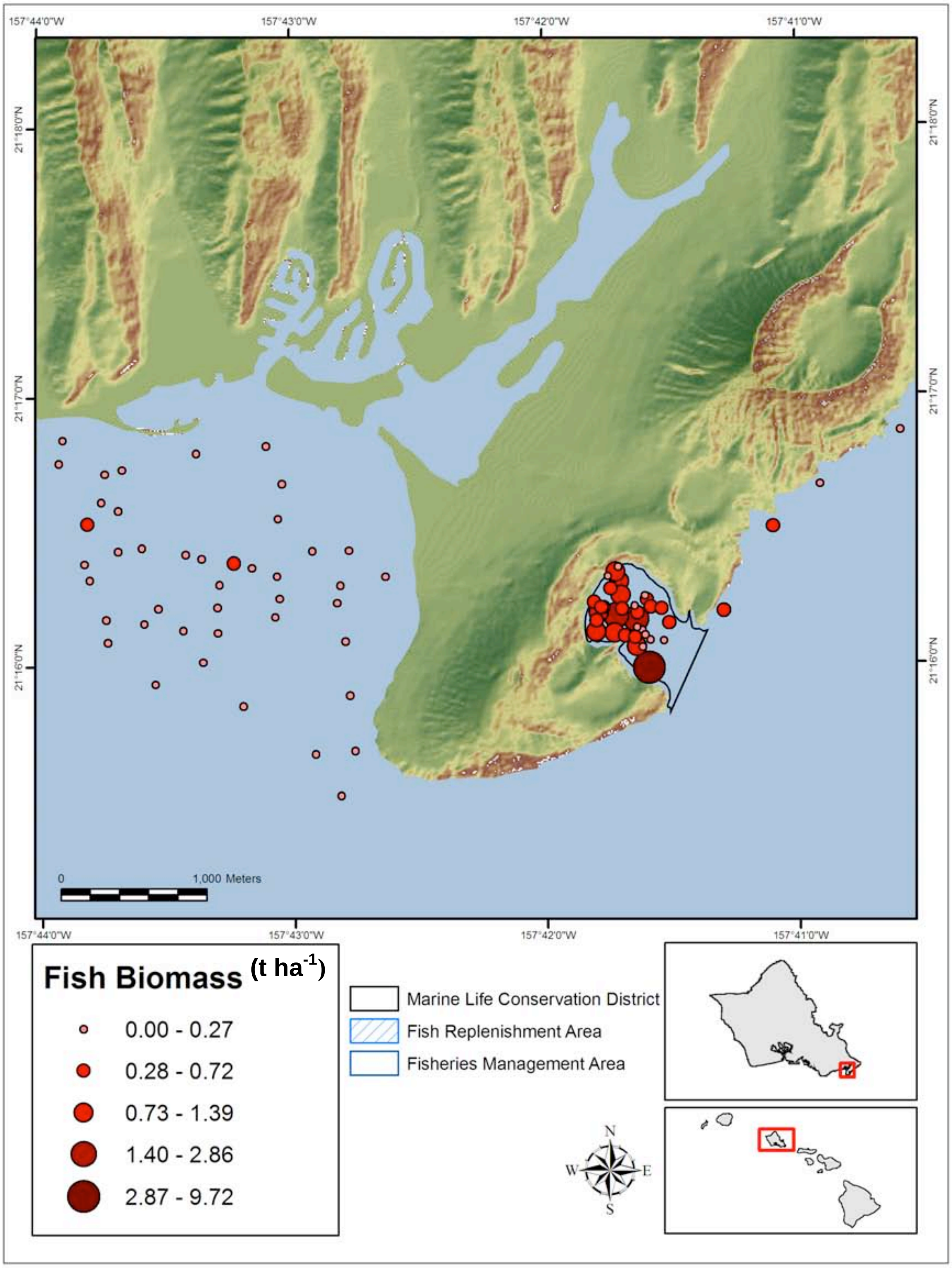

Figure 19. Fish biomass (t ha^{-1}) by individual transects (N=80) for southeast Oahu study area including Hanauma Bay MLCD. Classification based on quantiles.

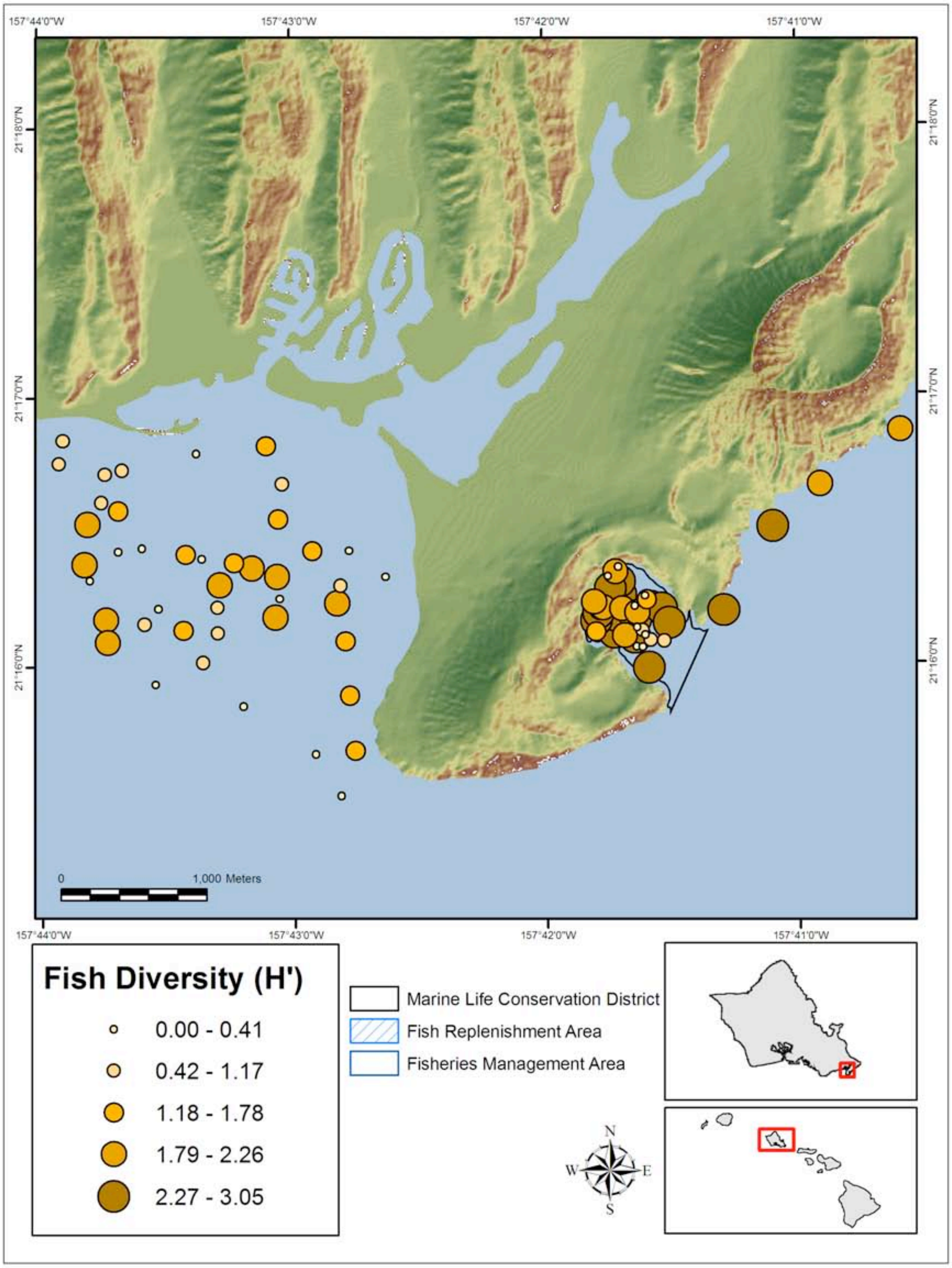

Figure 20. Fish diversity (H') by individual transects (N=80) for southeast Oahu study area including Hanauma Bay MLCD. Classification based on quantiles.

Table 13A. Comparison of fish species richness among management regimes and habitat types for the southeast Oahu study area including the Hanauma Bay MLCD. Results of nested ANOVA with major habitat types common to all management regimes nested within management regime (N = 69). Management regimes: MLCD ([M]), Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB), <10% live coral hard bottom (UCH), and unconsolidated sediment (UCS). Unplanned multiple comparisons among management strata and habitat$_{[\text{management}]}$ tested using Tukey's HSD tests. Underlined means are not significantly different ($\alpha = 0.05$)

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	878.5	56.7	<0.001	
Management	1	626.8	40.5	<0.001	MLCD > Open
Habitat$_{[\text{management}]}$	4	933.7	60.3	<0.001	
Error	63	15.5			
Habitat$_{[\text{management}]}$ -					CHB$_{[M]}$ UCH$_{[M]}$ CHB$_{[O]}$ UCH$_{[O]}$ UCS$_{[M]}$ UCS$_{[O]}$

Table 13B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the southeast Oahu study area, including Hanauma Bay MLCD. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	0.83	20.3	<0.0001	
Management	1	1.82	44.4	<0.0001	MLCD > Open
Habitat$_{[\text{management}]}$	4	0.56	13.7	<0.0001	
Error	63	0.04			
Habitat$_{[\text{management}]}$ -					CHB$_{[M]}$ UCH$_{[M]}$ CHB$_{[O]}$ UCH$_{O]}$ UCS$_{[M]}$ UCS$_{[O]}$

Table 13C. Comparison of fish species diversity (H') among management regimes and habitat types for the southeast Oahu study area, including Hanauma Bay MLCD.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	10.7	58.8	<0.001	
Management	1	3.8	20.7	<0.001	MLCD > Open
Habitat$_{[\text{management}]}$	4	12.6	69.4	<0.001	
Error	63	0.2			
Habitat$_{[\text{management}]}$ -					CHB$_{[M]}$ UCH$_{[M]}$ CHB$_{[O]}$ UCH$_{[O]}$ UCS$_{[M]}$ UCS$_{[O]}$

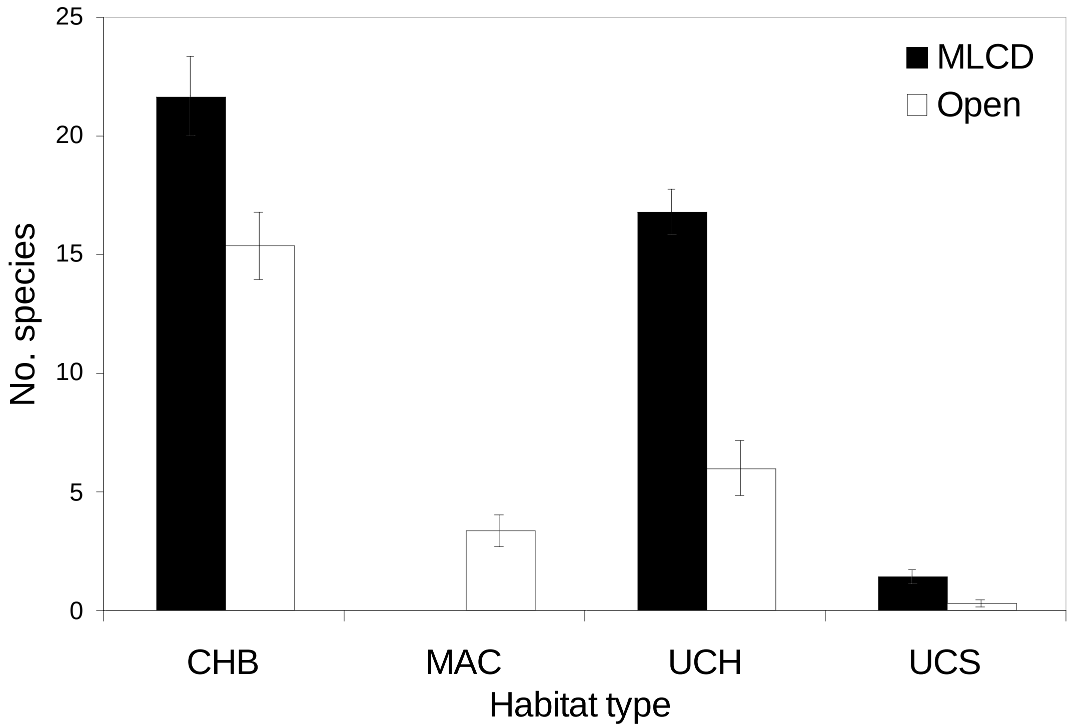

Figure 21. Mean number of species per transect (125 m^2) by habitat type and management regime for the southeast Oahu study area. Error bars are standard error of the mean.

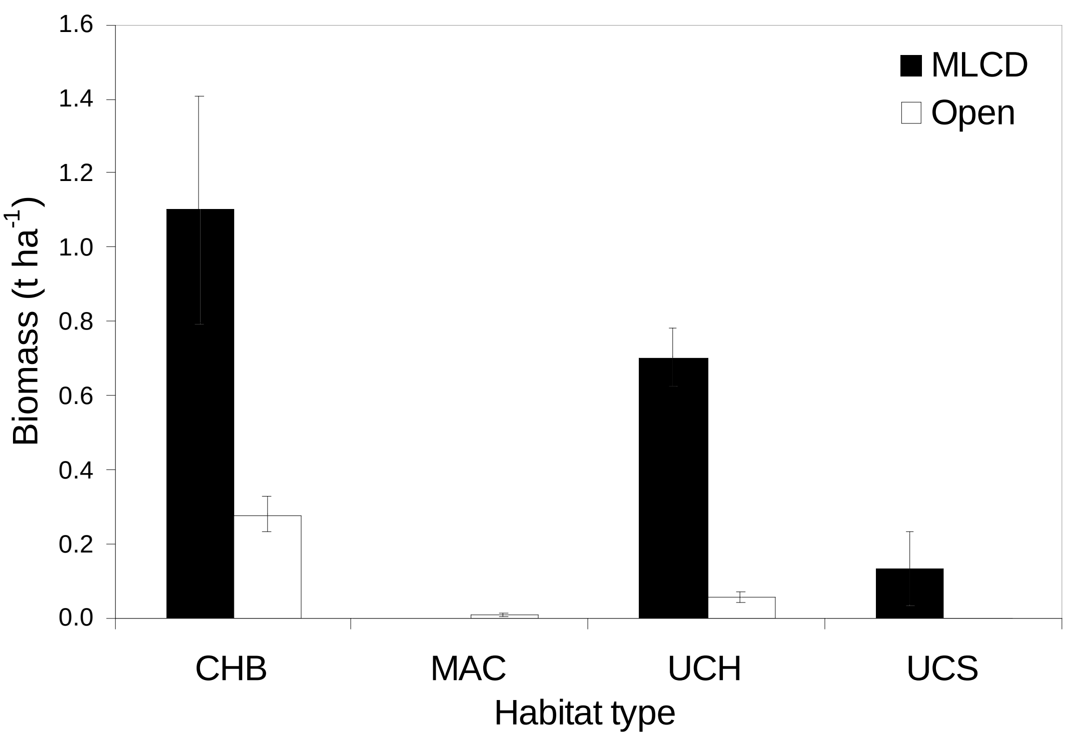

Figure 22. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the southeast Oahu study area. Error bars are standard error of the mean.

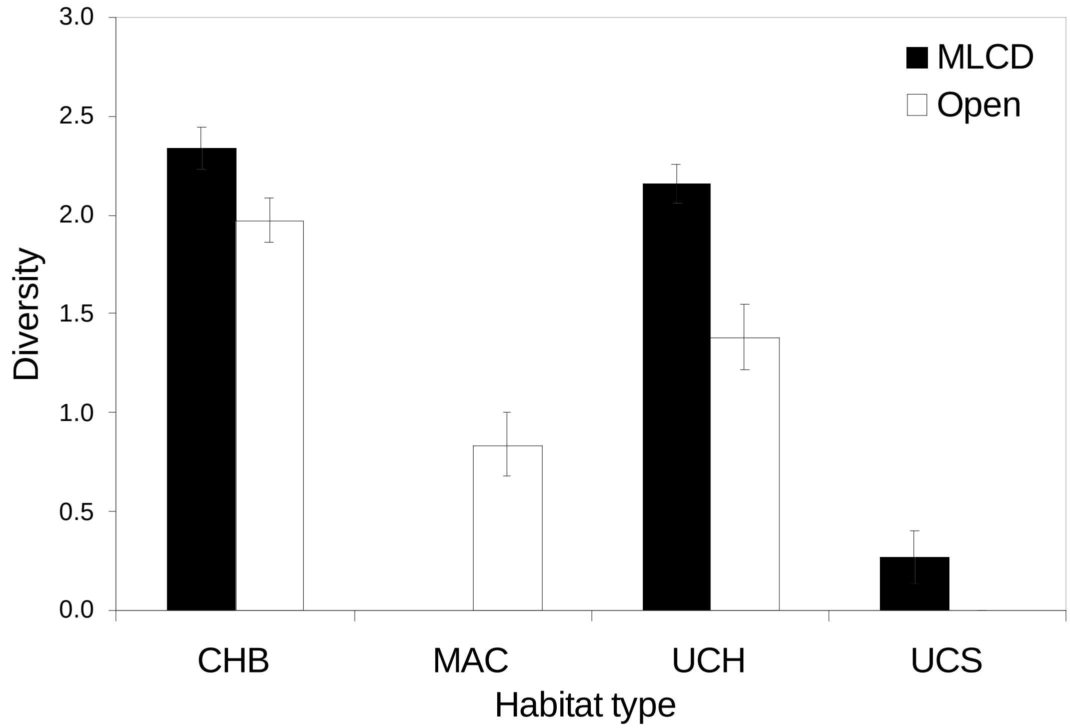

Figure 23. Mean diversity (H') per transect (125 m^2) by habitat type and management regime for the southeast Oahu study area. Error bars are standard error of the mean.

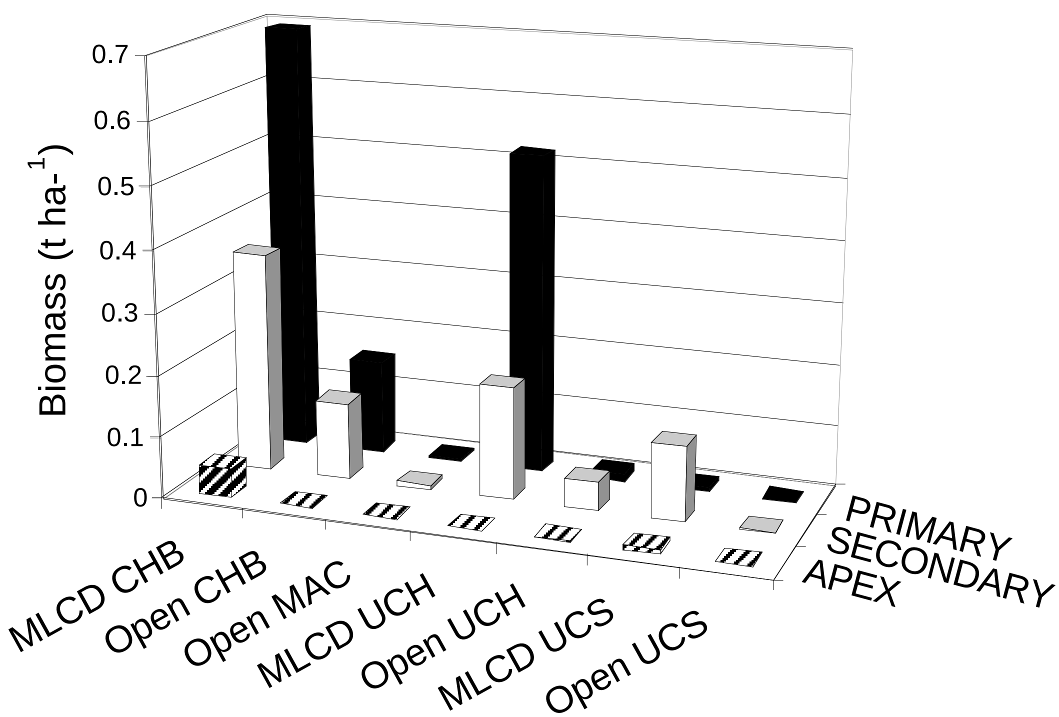

Figure 24. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the southeast Oahu study area.

Table 14. Top ten species in the Hanauma Bay MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Scarus psittacus	Palenose Parrotfish	*uhu*	0.71	0.058	54.55	15.11	8.75	477.51
Acanthurus triostegus	Convict Tang	*manini*	0.56	0.049	48.48	11.77	7.46	361.60
Mulloidichthys vanicolensis	Yellowfin Goatfish	*weke ula*	0.21	0.081	15.15	4.42	12.28	186.13
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.05	0.025	48.48	1.13	3.78	183.46
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.34	0.029	39.39	7.19	4.43	174.54
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.36	0.019	54.55	7.71	2.90	158.10
Melichthys niger	Black Durgon	*humuhumuelele*	0.11	0.079	9.09	2.26	12.04	109.45
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.34	0.008	66.67	7.14	1.25	83.49
Acanthurus nigroris	Bluelined Surgeonfish	*maiko*	0.06	0.012	36.36	1.28	1.75	63.67
Acanthurus achilles	Achilles Tang	*pakuikui*	0.09	0.017	21.21	1.85	2.64	56.10

Table 15. Top ten species in the southeast Oahu open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.28	0.007	46.81	15.28	7.94	371.48
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.19	0.009	31.91	10.28	10.55	336.79
Scarus psittacus	Palenose Parrotfish	*uhu*	0.19	0.009	25.53	10.09	10.30	262.94
Rhinecanthus rectangulus	Reef Triggerfish	*humuhumunukunukuapuaa*	0.03	0.005	29.79	1.57	5.86	174.49
Parupeneus multifasciatus	Manybar Goatfish	*moano*	0.05	0.005	25.53	2.69	5.68	144.92
Stethojulis balteata	Belted Wrasse	*omaka*	0.09	0.001	51.06	4.63	0.98	50.12
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.03	0.002	14.89	1.76	2.69	39.99
Chromis vanderbilti	Blackfin Chromis		0.39	0.001	27.66	21.30	1.40	38.76
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.03	0.003	8.51	1.67	4.01	34.14
Melichthys niger	Black Durgon	*humuhumuelele*	0.01	0.004	6.38	0.46	4.86	31.01

Pupukea MLCD and north shore Oahu
The north shore Oahu study area extended from Sunset Beach to Kawailoa Beach (ca. 6.5km) and included the Pupukea MLCD.

Sample allocation

A total of 73 samples were collected between June 12 and July 10, 2003 (Fig. 25; Table 16). The two levels of sampling stratification included major habitat types (CHB, MAC, UCH, and sand) and fisheries management regime (open access and MLCD). Macroalgae habitat was not present at the one-acre minimum mapping unit within the MLCD, and the colonized hardbottom habitat was likewise not present in the open area at the one-acre minimum mapping unit.

Table 16. Sample allocation for north shore Oahu study area.

Habitat	MLCD	Open	Total
Colonized hardbottom	9	-	9
Macroalgae	-	12	12
Uncolonized hardbottom	15	15	30
Sand	11	11	22
Total	35	38	73

Large-scale benthic cover

Benthic coverage for the Pupukea MLCD was derived from the NOAA benthic habitat maps with uncolonized volcanic rock/boulder accounting for 56% of the total habitat within the MLCD, followed by sand (30%), colonized volcanic rock/boulder (7%), and uncolonized pavement (7%) (Table17).

Table 17. Benthic cover for the Pupukea MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized hardbottom	Colonized volcanic rock/boulder	52766	7.43
Sand		211566	29.80
Uncolonized hardbottom	Uncolonized pavement	50405	7.10
	Uncolonized volcanic rock/boulder	395286	55.67
Grand total		710022	100.00

Small-scale benthic cover of substrate types within the management regimes.

Turf algae was the most abundant substrate type and averaged 44% cover in the MLCD and 53 % cover in the open access area (Table 18; Fig. 26). Sand cover was nearly equivalent in the MLCD (38%) and the open access areas (34%) compared to coralline algae which, was nearly 3 times more abundant in the MLCD (10%) than outside the reserve (4%). Similar to Hanauma Bay, macroalgal cover was higher in the open access area (6%) than in the MLCD (2%). Differences in macroalgal cover were primarily due to the abundance of *Microdictyon sp.* (2%), *Halimedia sp.* (1%), and *Acanthophora sp.* (1%) in the open access area (Table 18). *Galaxaura sp.* and *Turbinaria sp.* covered roughly equivalent portions of the substrate in the two management regimes. Total coral cover was 6% in the MLCD and 3% in the open area. *Porites lobata* (2%) and *Montipora patula* (2%) in the MLCD contributed to the difference in total coral cover between the two management strata. Macorinvertebrates comprised less than 1% of the benthic cover.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types even though cover of macroalgae and coralline algae were quite different between the MLCD and the open areas (Fig. 26). This result indicated that comparing fish assemblages across the management strata was appropriate at the major subtrate types.

Fish assemblage characteristics among habitat types and between management regimes

Fish assemblage characteristics were generally higher in the MLCD compared with open areas (Fig. 27, 28, and 29). Species richness was highest in the colonized MLCD habitat, followed by uncolonized MLCD and uncolonized open areas (Fig. 30). The uncolonized and colonized MLCD habitats had the highest fish biomass observed over the area, respectively (Fig. 31). Diversity was similar among colonized, uncolonized, and macroalgae habitat types (Fig. 32). Within the habitat types common to both management strata, richness and biomass were significantly greater ($p<0.05$) in the MLCD, while diversity was not significantly different (Table 19A, 19B, and 19C).

Fish trophic structure between management regimes and among habitats

Primary consumers accounted for 74% of the biomass in the MLCD but only 40% in the open area (Fig. 33). Additionally, they were seven times more abundant by weight in the MLCD. Secondary consumers comprised 60% of the biomass in the open area but were 1.6 times less abundant by weight compared to the MLCD. Apex predator biomass was similar but low for both management strata.

Species composition by management regime

Three large surgeonfish, whitebar surgeonfish (*maikoiko*, *Acanthurus leucopareius*), orangeband surgeonfish (*naenae*, *A. olivaceus*), and orangespine unicornfish (*umaumalei*), accounted for more than 41% of the total fish biomass in the MLCD (Table 20). Another prized species, lowfin chub (*nenue*, *Kyphosus* spp.) comprised an additional 10% of the biomass. In the open area, small wrasses were most common but a few resource species, such as whitebar surgeonfish (*maikoiko*), manybar goatfish (*moano*, *Parupeneus multifasciatus*), and convict tang (*manini*), were encountered with some frequency (Table 21).

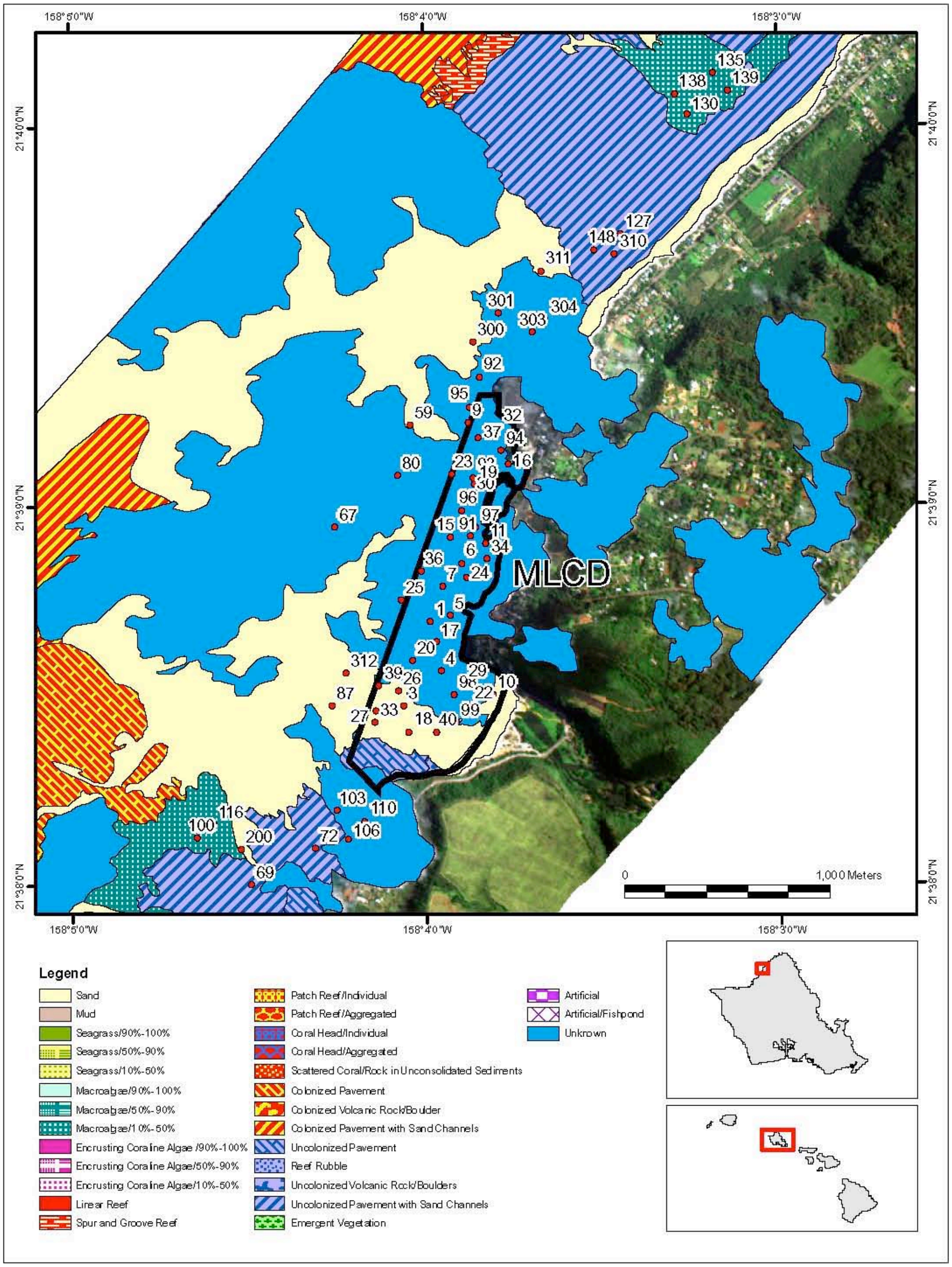

Figure 25. Sampling locations and benthic habitats for the Pupukea MLCD and adjacent areas.

Table 18. Top 10 benthic taxa/substrate types by percent cover within the Pupukea Marine Life Conservation District (MLCD) and the open access area (Open) outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		44.3	Turf algae		52.8
Sand		37.6	Sand		33.7
Coralline algae		10.3	Coralline algae		3.7
Coral	*Porites lobata*	2.4	Macroalgae	*Microdictyon sp.*	1.8
Coral	*Montipora patula*	1.6	Coral	*Porites lobata*	1.3
Macroalgae	*Galaxaura sp.*	0.9	Macroalgae	*Halimeda sp.*	0.9
Coral	*Montipora flabellata*	0.8	Macroalgae	*Galaxaura sp.*	0.8
Coral	*Pocillopora meandrina*	0.6	Coral	*Montipora capitata*	0.7
Coral	*Montipora capitata*	0.6	Macroalgae	*Acanthophora sp.*	0.7
Macroalgae	*Turbinaria sp.*	0.5	Macroalgae	*Turbinaria sp.*	0.7

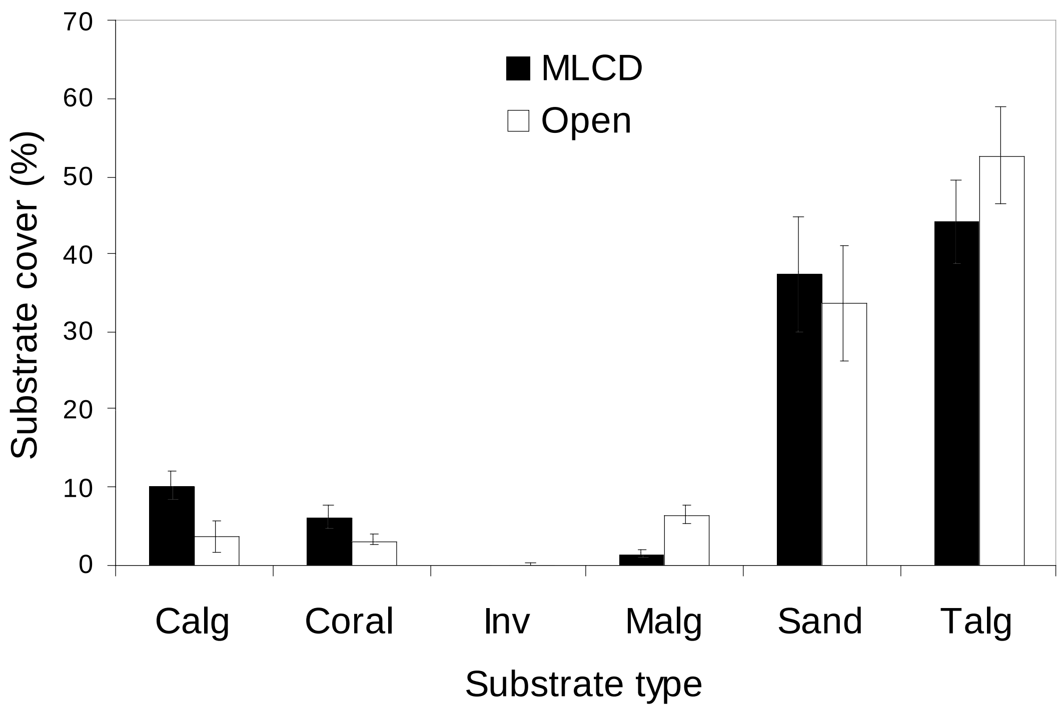

Figure 26. Mean percent cover of substrate types within the Pupukea Marine Life Conservation District (MLCD) and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

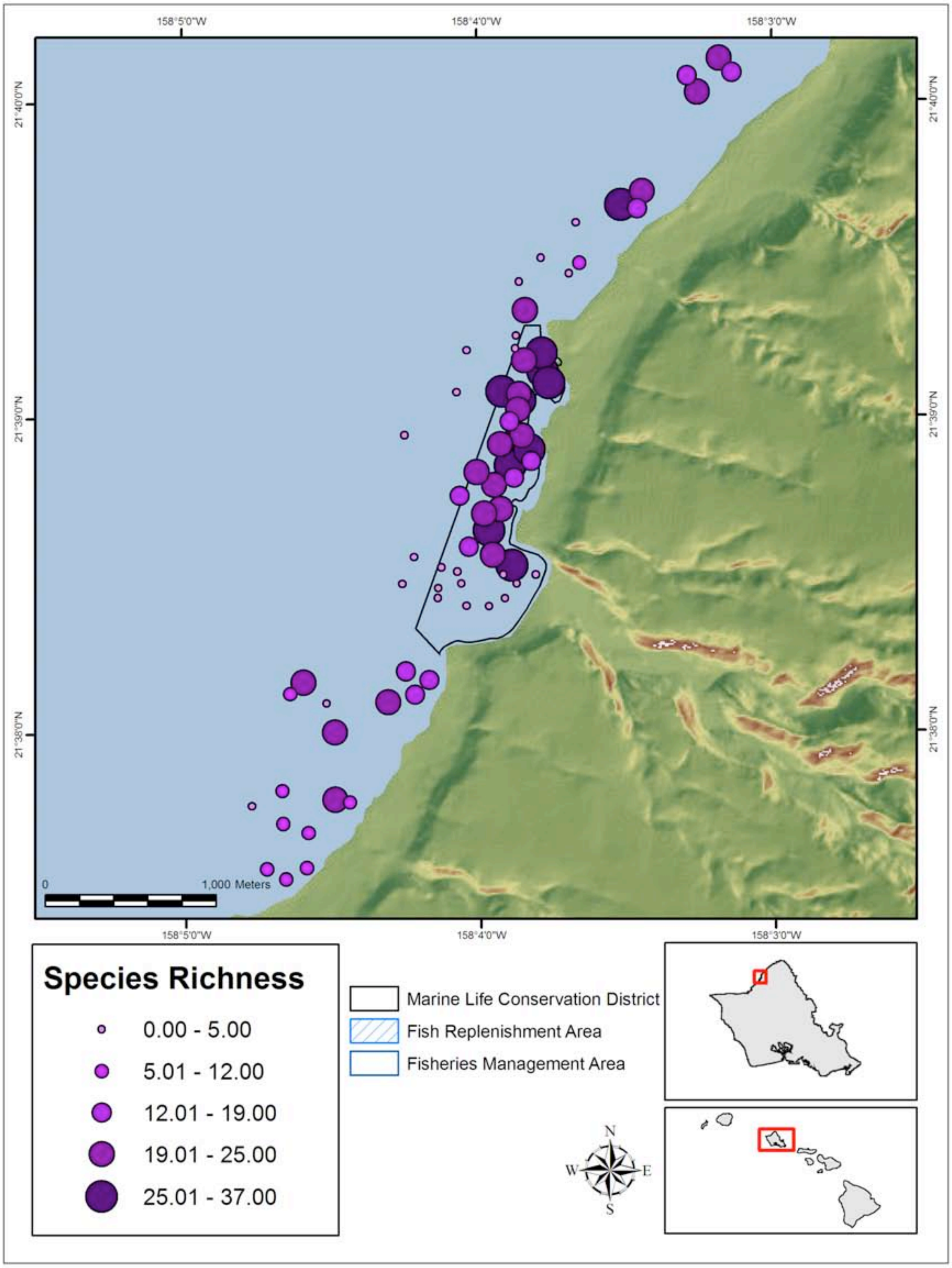

Figure 27. Species richness by individual transects (N=73) for the north shore Oahu study area including Pupukea MLCD. Classification based on quantiles.

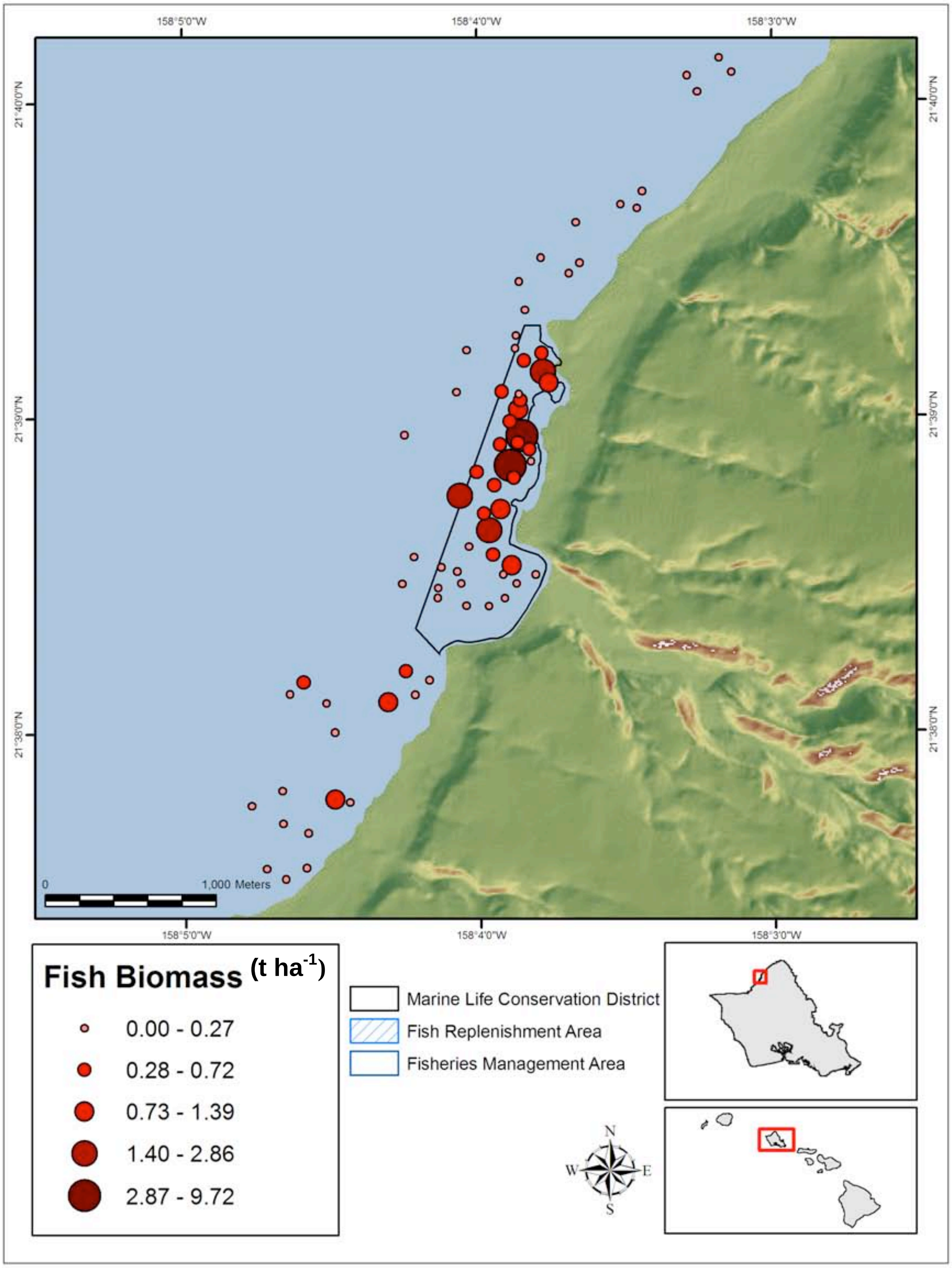

Figure 28. Fish biomass (t ha^{-1}) by individual transects (N=73) for the north shore Oahu study area including Pupukea MLCD. Classification based on quantiles.

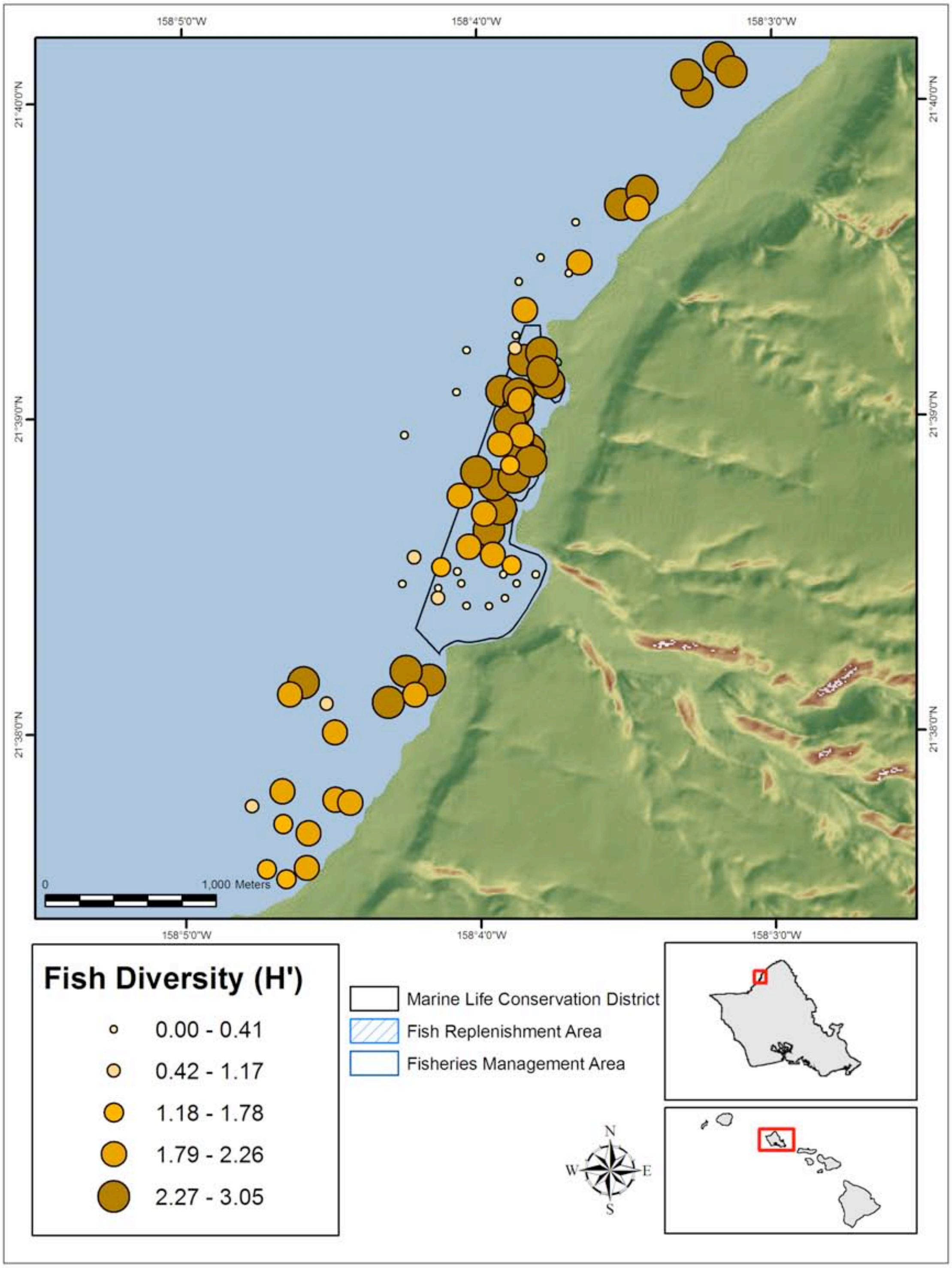

Figure 29. Fish diversity (H') by individual transects (N=73) for the north shore Oahu study area including Pupukea MLCD. Classification based on quantiles.

Table 19A. Comparison of fish species richness among management regimes and habitat types for the north shore Oahu study area, including the Pupukea MLCD. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 52). Management regimes: MLCD ([M]) and Open (completely open to fishing ([O])). Habitat strata: <10% live coral hard bottom (UCH) and Sand. Unplanned multiple comparisons among management strata and habitat$_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different (α = 0.05)

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	1625.5	74.8	<0.001	
Management	1	117.50	5.4	0.024	MLCD > Open
Habitat$_{[management]}$	2	2356.0	108.4	<0.001	
Error	48	21.70			
Habitat$_{[management]}$ -					$UCH_{[M]}$ $UCH_{[O]}$ $\underline{UCS_{[M]}\ \ UCS_{[O]}}$

Table 19B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the southeast Oahu study area, including Hanauma Bay MLCD. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	1.06	12.9	<0.0001	
Management	1	0.37	4.5	0.038	MLCD > Open
Habitat$_{[management]}$	2	1.35	16.2	<0.0001	
Error	48	0.08			
Habitat$_{[management]}$ -					$UCH_{[M]}$ $UCH_{O]}$ $\underline{UCS_{[M]}\ \ UCS_{[O]}}$

Table 19C. Comparison of fish species diversity (H') among management regimes and habitat types for the southeast Oahu study area, including Hanauma Bay MLCD.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	16.80	67.7	<0.001	
Management	1	0.22	0.87	0.354	MLCD = Open
Habitat$_{[management]}$	2	25.10	101.0	<0.001	
Error	48	0.25			
Habitat$_{[management]}$ -					$\underline{UCH_{[M]}\ \ UCH_{[O]}}$ $\underline{UCS_{[M]}\ \ UCS_{[O]}}$

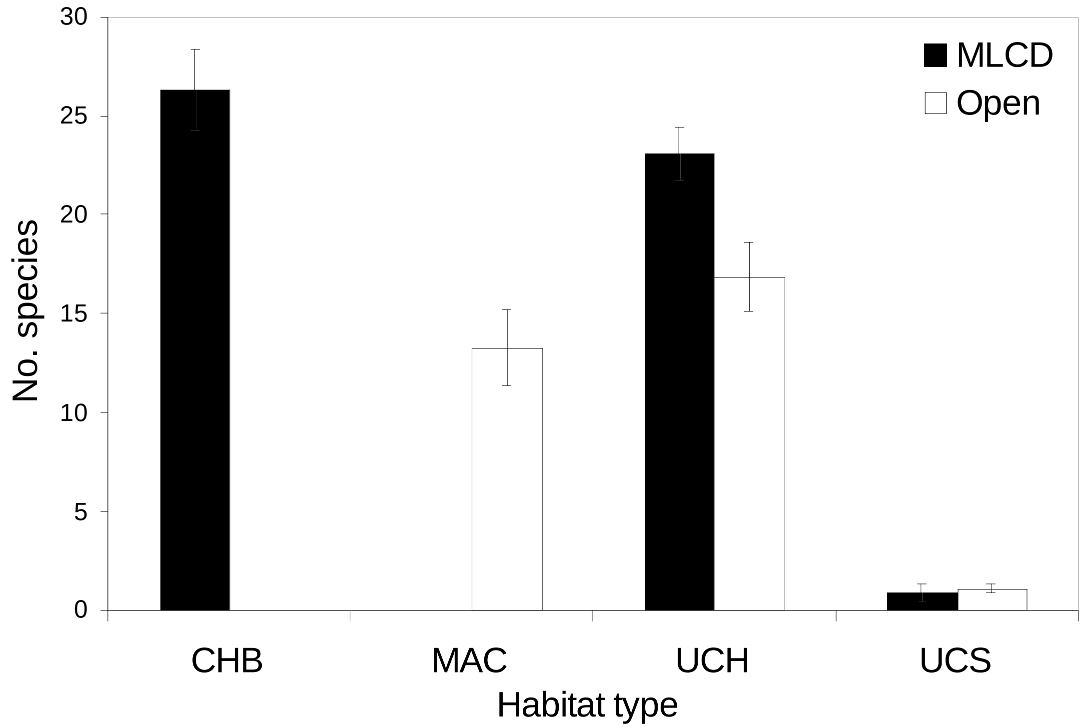

Figure 30. Mean number of species per transect (125 m^2) by habitat type and management regime for the north shore Oahu study area. Error bars are standard error of the mean.

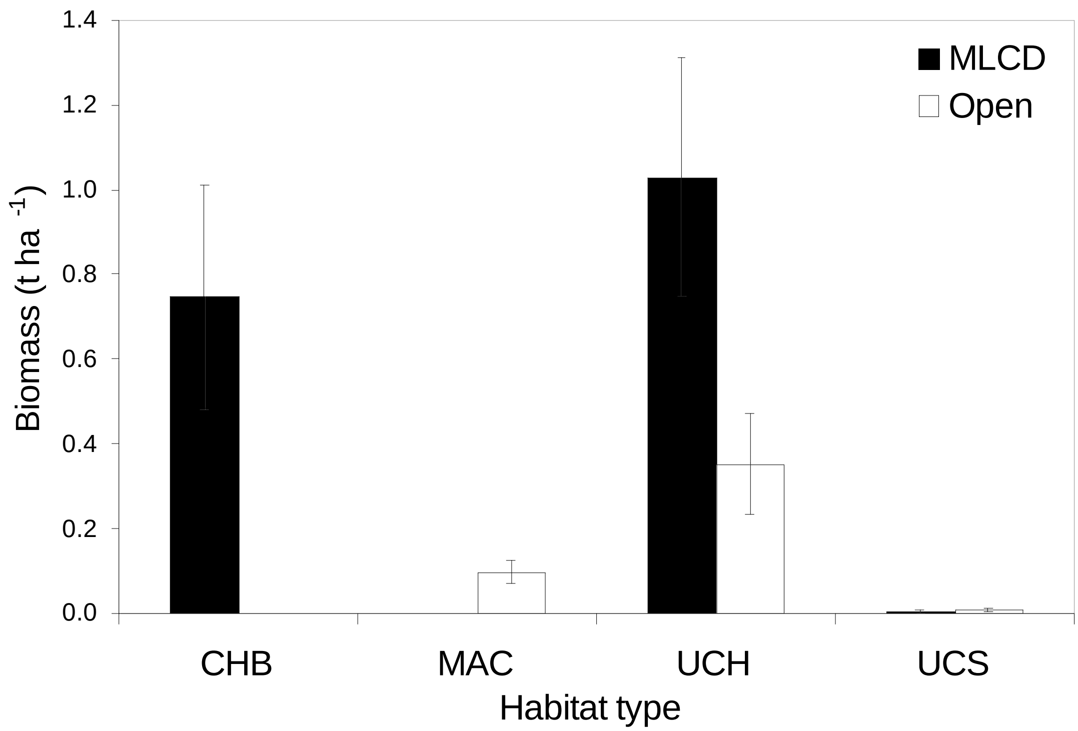

Figure 31. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the north shore Oahu study area. Error bars are standard error of the mean.

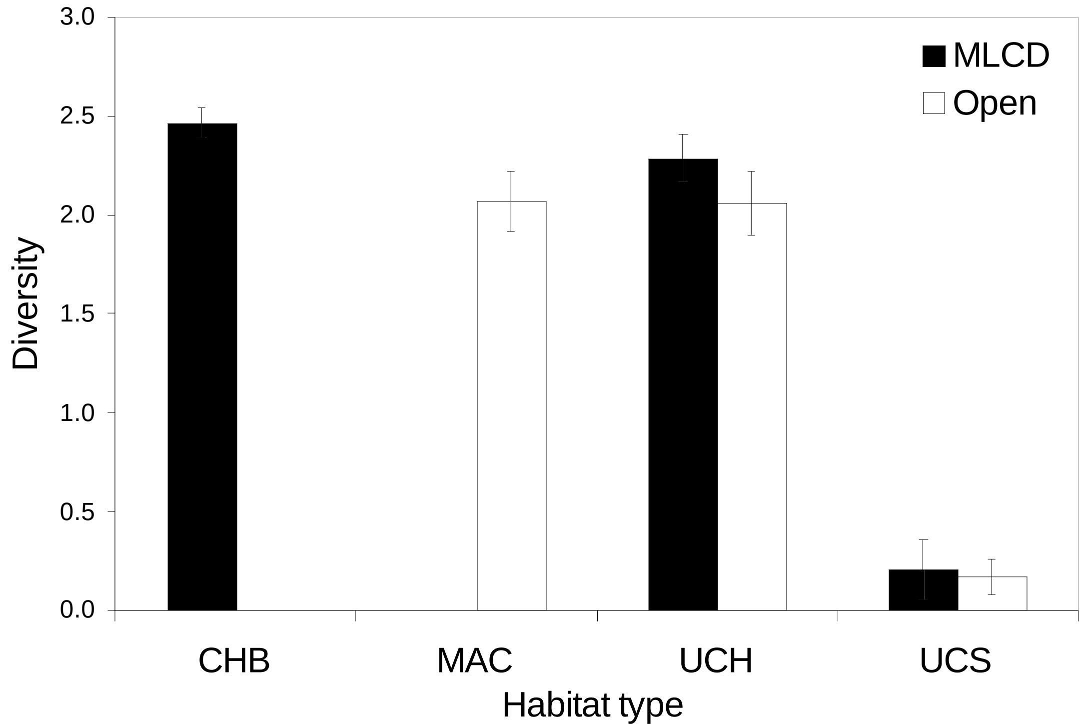

Figure 32. Mean diversity (H’) per transect (125 m^2) by habitat type and management regime for the north shore Oahu study area. Error bars are standard error of the mean.

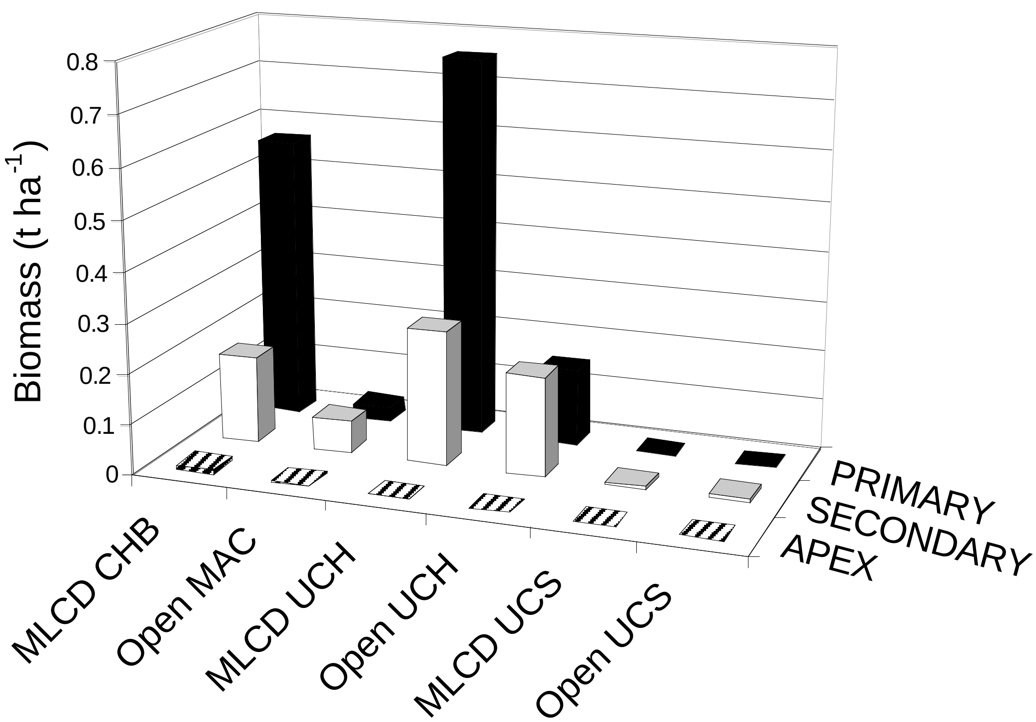

Figure 33. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the north shore Oahu study area.

Table 20. Top ten species in the Pupukea MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.68	0.183	37.14	9.36	28.82	1070.45
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.77	0.042	68.57	10.65	6.62	453.80
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.13	0.052	31.43	1.82	8.15	256.06
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.06	0.030	42.86	0.85	4.71	201.97
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.72	0.014	68.57	9.92	2.14	146.72
Kyphosus species	Lowfin Chub	*nenue*	0.13	0.064	11.43	1.79	10.13	115.78
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.17	0.018	40.00	2.39	2.89	115.77
Chromis ovalis	Oval Chromis		0.76	0.019	28.57	10.49	2.93	83.57
Acanthurus triostegus	Convict Tang	*manini*	0.32	0.026	20.00	4.33	4.12	82.45
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.08	0.010	48.57	1.13	1.60	77.64

Table 21. Top ten species in the north shore Oahu open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.61	0.008	65.79	13.87	4.90	322.07
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.24	0.009	44.74	5.48	5.42	242.41
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.10	0.022	15.79	2.19	12.56	198.29
Stegastes fasciolatus	Pacific Gregory		0.24	0.005	44.74	5.48	2.85	127.52
Parupeneus multifasciatus	Manybar Goatfish	*moano*	0.09	0.005	39.47	1.95	3.02	119.25
Rhinecanthus rectangulus	Reef Triggerfish	*humuhumunukunukuapuaa*	0.04	0.006	34.21	0.95	3.40	116.35
Acanthurus triostegus	Convict Tang	*manini*	0.19	0.006	31.58	4.39	3.53	111.36
Coris venusta	Elegant Coris		0.33	0.004	52.63	7.58	2.04	107.38
Stethojulis balteata	Belted Wrasse	*omaka*	0.47	0.003	55.26	10.53	1.63	89.83
Acanthurus dussumieri1	Eye-stripe Surgeonfish	*palani*	0.04	0.011	13.16	0.95	6.44	84.77

Moku o Loe - University of Hawaii Marine Laboratory Refuge and Kaneohe Bay
The Kaneohe Bay study area included the entire bay shoreward of the barrier reef (ca. 14.1km) and included *Moku o Loe* - the University of Hawaii's Marine Laboratory Refuge (MLR).

Sample allocation

A total of 104 samples were collected in Kaneohe Bay from October 21 to November 1, 2002 (Fig. 34A and 34B; Table 22). In addition to the major habitat types, sampling locations were further stratified by reef morphology. Owing to the uniqueness of the environment in Kaneohe Bay, we considered patch reefs and linear reefs within Kaneohe Bay as separate strata.

Table 22. Sample allocation for Kaneohe Bay study area. MLR = University of Hawaii's Marine Laboratory Refuge

Habitat	Subhabitat	MLR	Open	Total
Colonized hardbottom	Linear reef		9	9
Macroalgae	Linear reef		12	12
Uncolonized hardbottom	Linear reef		10	10
Sand	Linear reef		10	10
Colonized hardbottom	Patch reef	20	21	41
Macroalgae	Patch reef	10	12	22
Total	Total	30	74	104

Large-scale benthic cover

Benthic coverage for the University of Hawaii's Marine Laboratory Refuge was derived from the NOAA benthic habitat maps and consisted of 82% colonized hardbottom and 18% mud (Table 23).

Table 23. Benthic cover for the University of Hawaii's Marine Laboratory Refuge derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Unconsolidated Sediment	Mud	52572	17.75
Colonized hardbottom	Reef/Patch Reef (Individual)	243633	82.25
Grand total		296206	100.00

Small-scale benthic cover of substrate types within the management regimes.

In Kaneohe Bay, coral cover (32%) and unconsolidated sediment (sand – 21%, silt – 7%, and mud – 4%) were the most abundant substrate types in the Marine Laboratory Refuge (MLR) (Table 24; Fig. 35). Unconsolidated sediment (sand – 27% and mud – 5%) was also abundant in the open access area but turf algae (23%) and macroalgae (22%) were also prevalent and there was lower coral cover (18%) than the MLR. In comparison, macroalgae (17%) and turf algae (13%) occupied less of the benthos in the MLR than in the open access areas. Macroalgae communities had similarities (e.g. *Dictyosphaeria sp.* and *Kappaphycus sp*) and differences (e.g. *Acanthophora sp., Gracilaria sp.,* and *Sargassum sp.*) between the two management regimes even though overall cover was roughly equivalent. *Porites compressa* and *Montipora capitata* were the predominant corals in both the MLR (25%, 7%) and the open access area (13%, 4%). Coralline algae cover was low (<5%) in both strata. Cover of macorinvertebrates was also low but some sponges (1%) were observed in the MLR. Two transects in the open access area documented high levels of *Halophila hawaiiensis* in the sand habitat but overall cover was low (0.3%).

Different management regimes had statistically similar levels of percent cover for each of the 7 substrate types (Fig. 35). This result indicated that comparing fish assemblages across the management strata was appropriate at the level of major subtrate types.

<u>Fish assemblage characteristics among habitat types</u>
The colonized hardbottom patch reefs harbored the highest species richness, numerical abundance, and biomass among all habitat types examined in Kaneohe Bay (Fig. 36, 37, and 38). Macroalgae dominated habitats had relatively low species richness (Fig. 39), extremely low biomass (Fig. 40), and moderate diversity (Fig. 41). Very few fishes were observed in sand habitat.

There were no significant differences (p>0.05) in species richness or biomass between the Marine Laboratory Refuge and patch reefs open to fishing for the two habitat types common to all patch reefs surveyed (Table 25A and 25B). Colonized hardbottom patch reefs, regardless of protection from fishing, had significantly more species and biomass than the macroalgae dominated patch reefs. Diversity was significantly higher in the Marine Laboratory Refuge compared to open areas (Table 25C).

<u>Fish trophic structure between management regimes and among habitats</u>
Herbivores accounted for more than 75% of the total fish biomass observed in Kaneohe Bay (Fig. 42). Secondary consumers comprised an additional 24%, while apex predators accounted for less than 0.5% of the total fish biomass in Kaneohe Bay. The Marine Laboratory Refuge and open area patch reefs had similar proportions of herbivores (76%, 73%) and secondary consumers (24%, 27%).

<u>Species composition by management regime</u>
Parrotfish comprised the majority of the fish biomass in the bay regardless of management strata with juveniles contributing greatly to the numerical abundance and biomass among all habitats. The endemic Spectacled parrotfish (*uhu uliuli*, *Chlorurus perspicillatus*) accounted for 28% of the total fish biomass in the Marine Laboratory Refuge, but only 7% in open areas (Tables 26). The bullethead parrotfish (*uhu*, *C. sordidus*) comprised an additional 10% of the biomass in the Refuge and was an important component of the fish assemblage, by weight, in the open areas (18%, Table 27). The palenose parrotfish (*uhu*, *Scarus psittacus*) was the most dominant species in the open area, based on IRD, and accounted for 21% of total fish biomass in this management stratum.

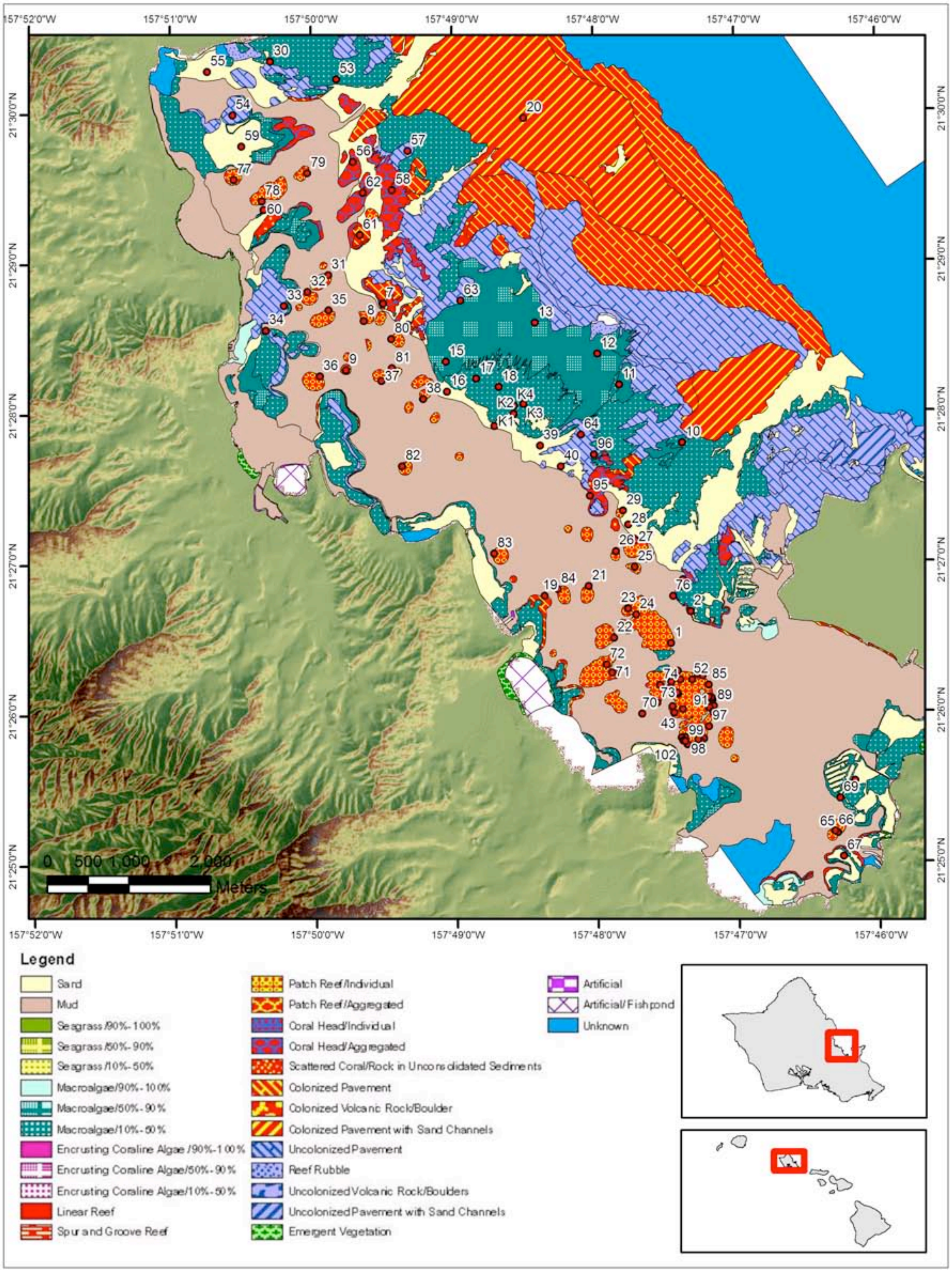

Figure 34A. Sampling locations and benthic habitats for the Kaneohe Bay study area.

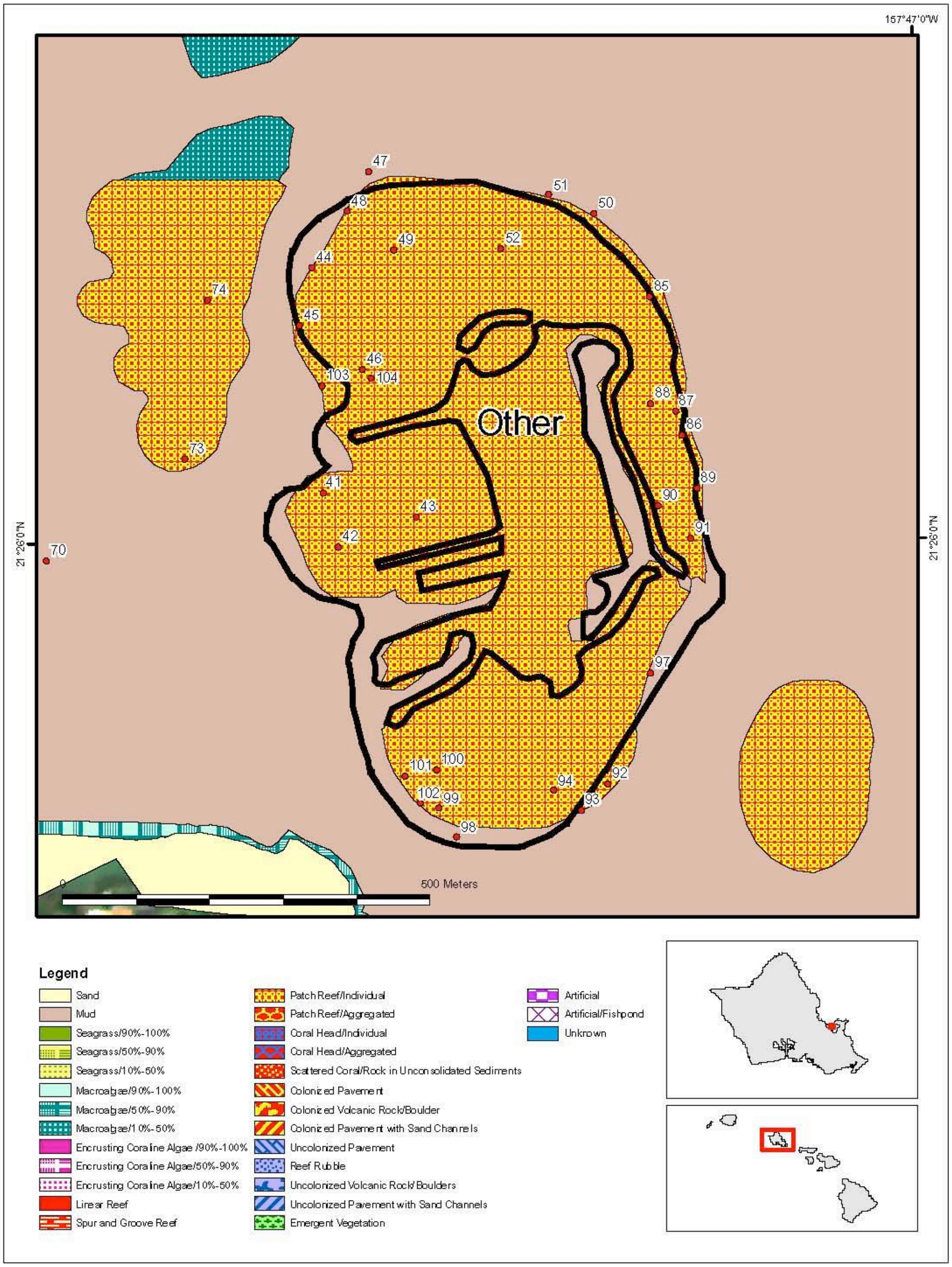

Figure 34B. Sampling locations and benthic habitats for the Moku o Loe – the University of Hawaii Marine Laboratory Refuge.

Table 24. Top 10 benthic taxa/substrate types by percent cover within the Marine Laboratory Refuge (MLR) and the open access area outside the refuge.

MLR			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Coral	*Porites compressa*	24.6	Sand		27.1
Sand		20.9	Turf algae		23.3
Turf algae		12.9	Coral	*Porites compressa*	13.0
Coral	*Montipora capitata*	7.4	Macroalgae	*Acanthophora sp.*	7.8
Silt		6.9	Macroalgae	*Dictyosphaeria sp.*	5.6
Macroalgae	*Dictyosphaeria sp.*	6.6	Mud		5.0
Macroalgae	*Gracilaria sp.*	6.0	Coralline algae		4.9
Coralline algae		4.7	Coral	*Montipora capitata*	3.5
Mud		4.1	Macroalgae	*Kappaphycus sp.*	2.8
Macroalgae	*Kappaphycus sp.*	2.8	Macroalgae	*Sargassum sp.*	2.4

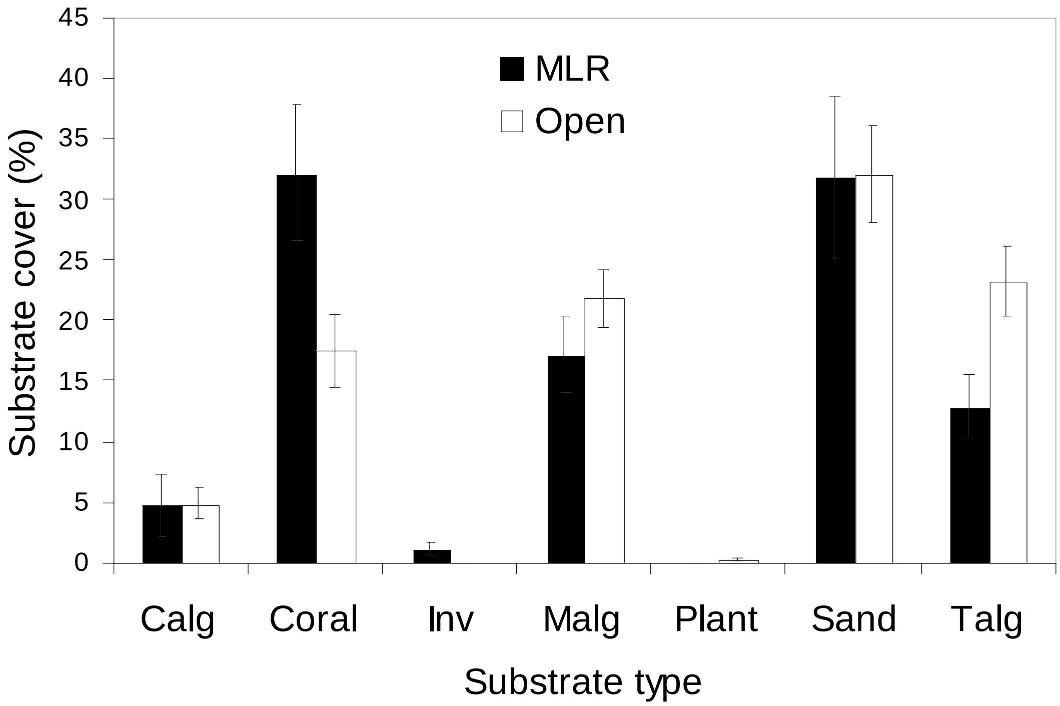

Figure 35. Mean percent cover of substrate types within the University of Hawaii Marine Laboratory Refuge (MLR) and outside (Open) of the MLR. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Silt and Mud, Talg = Turf algae. Error bars are ± 1 SE of the mean.

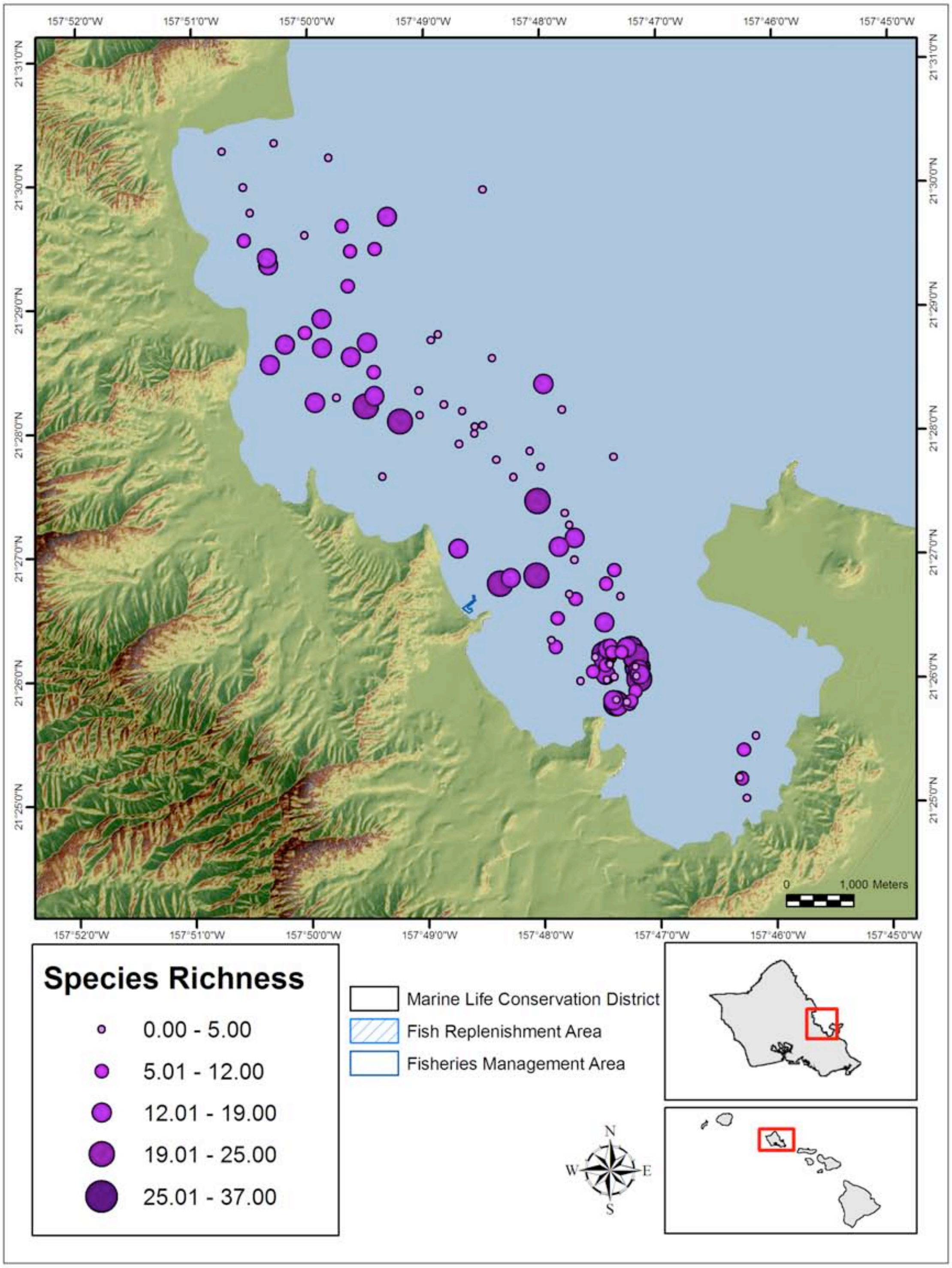

Figure 36. Species richness by individual transects (N=104) for the Kaneohe Bay study area, including UH Marine Laboratory Refuge. Classification based on quantiles.

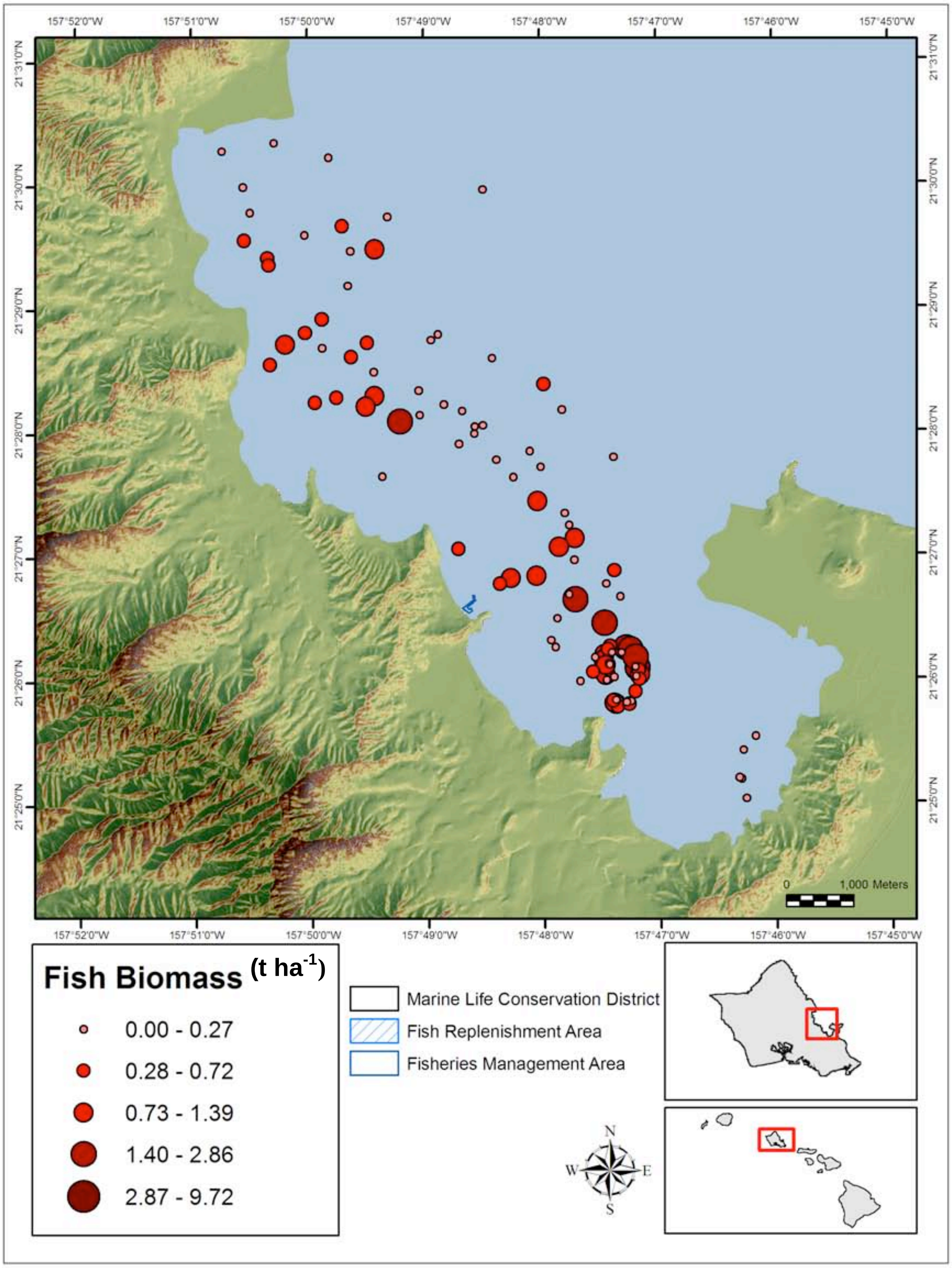

Figure 37. Fish biomass (t ha^{-1}) by individual transects (N=104) for the Kaneohe Bay study area, including UH Marine Laboratory Refuge. Classification based on quantiles.

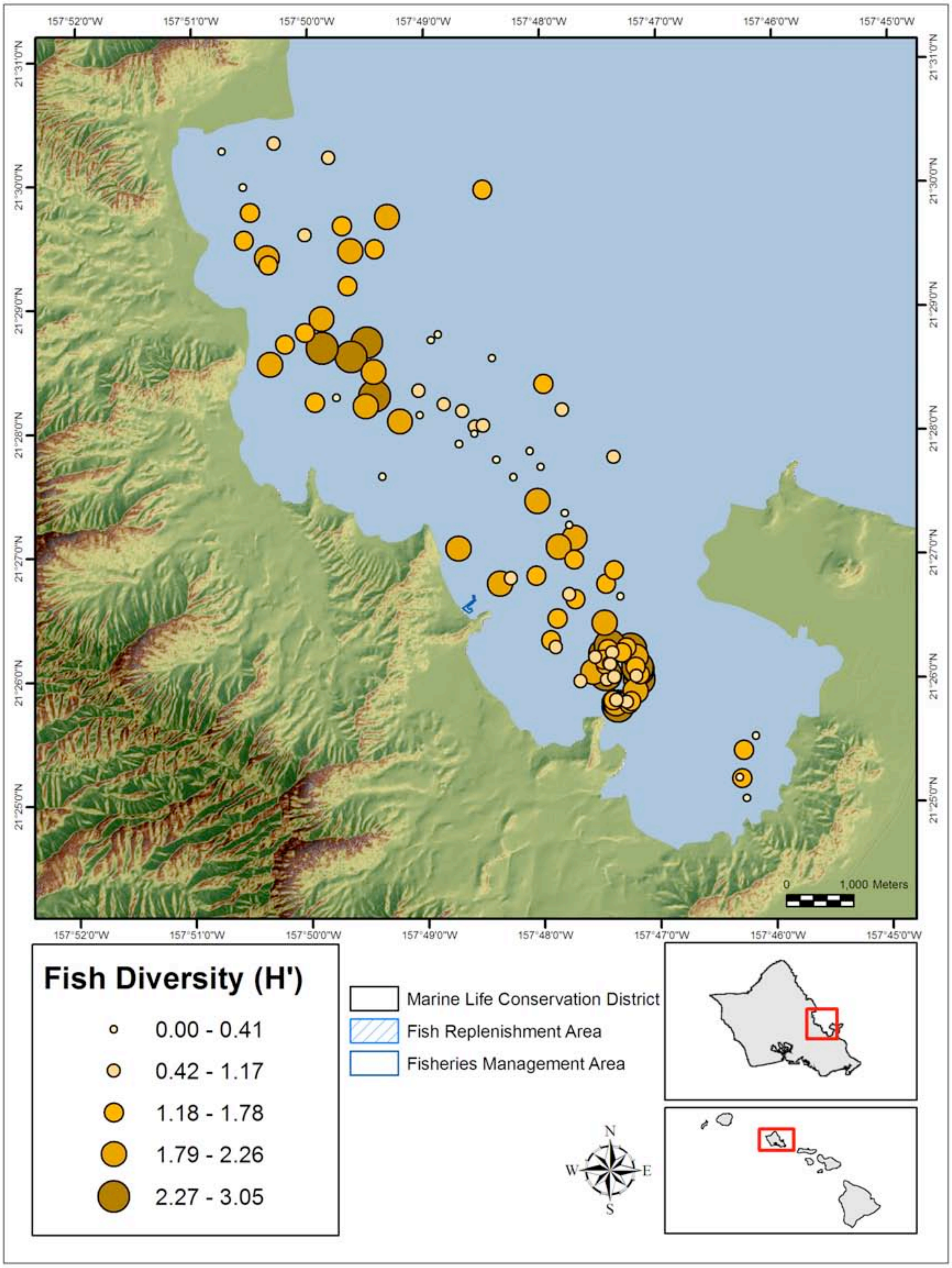

Figure 38. Fish diversity (H') by individual transects (N=104) for the Kaneohe Bay study area, including UH Marine Laboratory Refuge. Classification based on quantiles.

Table 25A. Comparison of fish species richness among management regimes and habitat types for the Kaneohe Bay study area, including the University of Hawaii Marine Laboratory Refuge (MLR). Results of nested ANOVA with major habitat types common to all management regimes nested within management regime (N =84). Management regimes: Marine Laboratory Refuge ([M]) and Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB) and Macroalgae (MAC). Unplanned multiple comparisons among management strata and $\text{habitat}_{[\text{management}]}$ tested using Tukey's HSD tests. Underlined means are not significantly different (α = 0.05)

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	1060	77.4	<0.001	
Management	1	42	3.1	0.080	MLR = Open
$\text{Habitat}_{[\text{management}]}$	2	1499	109.6	<0.001	
Error	80	14			
$\text{Habitat}_{[\text{management}]}$ -					$\underline{CHB_{[M]}\ \ CHB_{[O]}}$ $\underline{MAC_{[M]}\ \ MAC_{[O]}}$

Table 25B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the Kaneohe Bay study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	2.0	47.2	<0.001	
Management	1	0.1	2.3	0.130	MLR = Open
$\text{Habitat}_{[\text{management}]}$	2	2.8	62.1	<0.0001	
Error	80	0.1			
$\text{Habitat}_{[\text{management}]}$ -					$\underline{CHB_{[M]}\ \ CHB_{[O]}}$ $\underline{MAC_{[O]}\ \ MAC_{[O]}}$

Table 25C. Comparison of fish species diversity (H') among management regimes and habitat types for the Kaneohe Bay study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	9.8	56.1	<0.001	
Management	1	0.7	4.4	0.040	MLR > Open
$\text{Habitat}_{[\text{management}]}$	2	13.7	78.1	<0.001	
Error	80	0.2			
$\text{Habitat}_{[\text{management}]}$ -					$\underline{CHB_{[M]}\ \ CHB_{[O]}}$ $\underline{MAC_{[M]}\ \ MAC\ _{[O]}}$

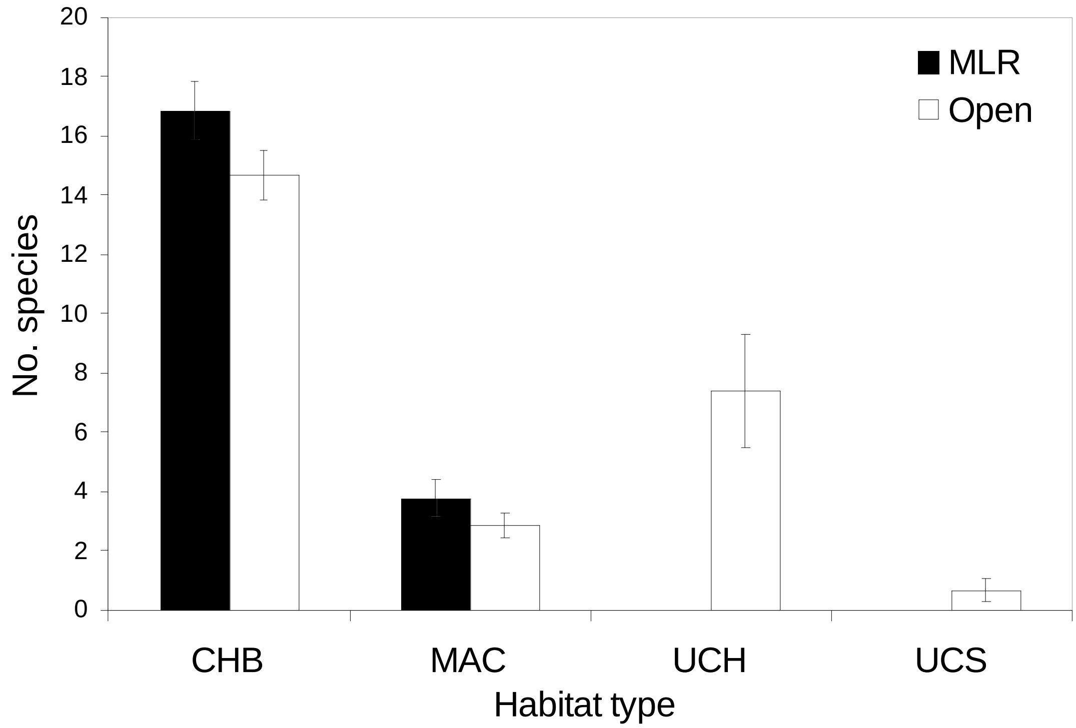

Figure 39. Mean number of species per transect (125 m^2) by habitat type and management regime for the Kaneohe Bay study area. Error bars are standard error of the mean. MLR = University of Hawaii Marine Laboratory Refuge.

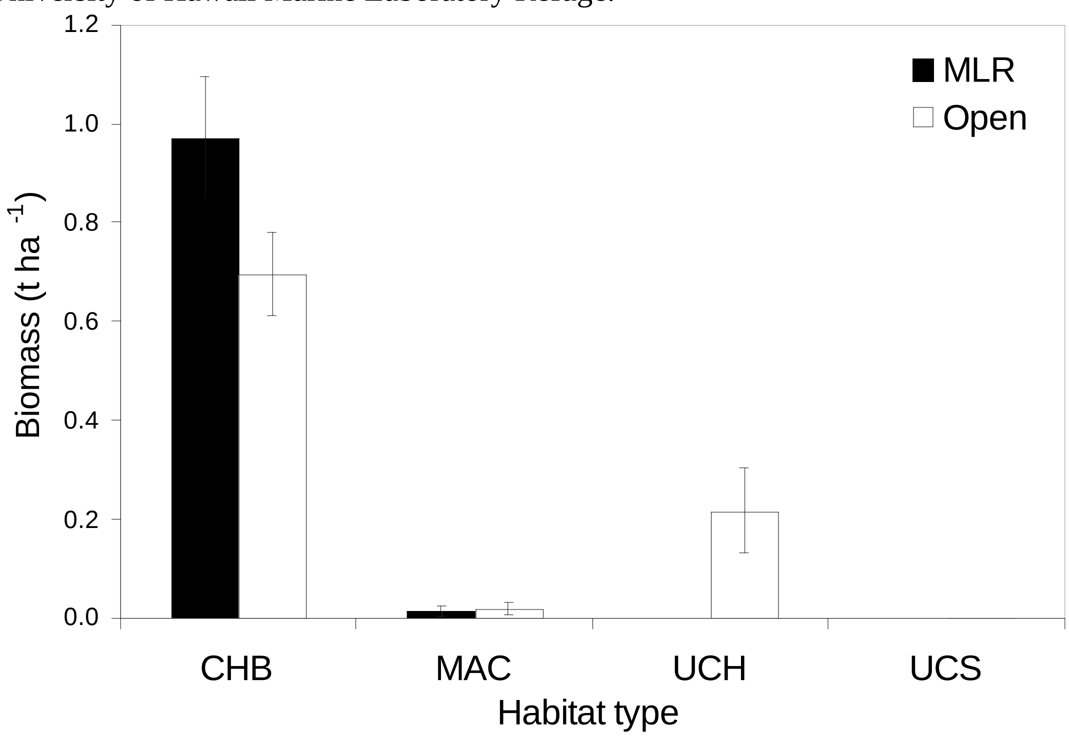

Figure 40. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the Kaneohe Bay study area. Error bars are standard error of the mean. MLR = University of Hawaii Marine Laboratory Refuge.

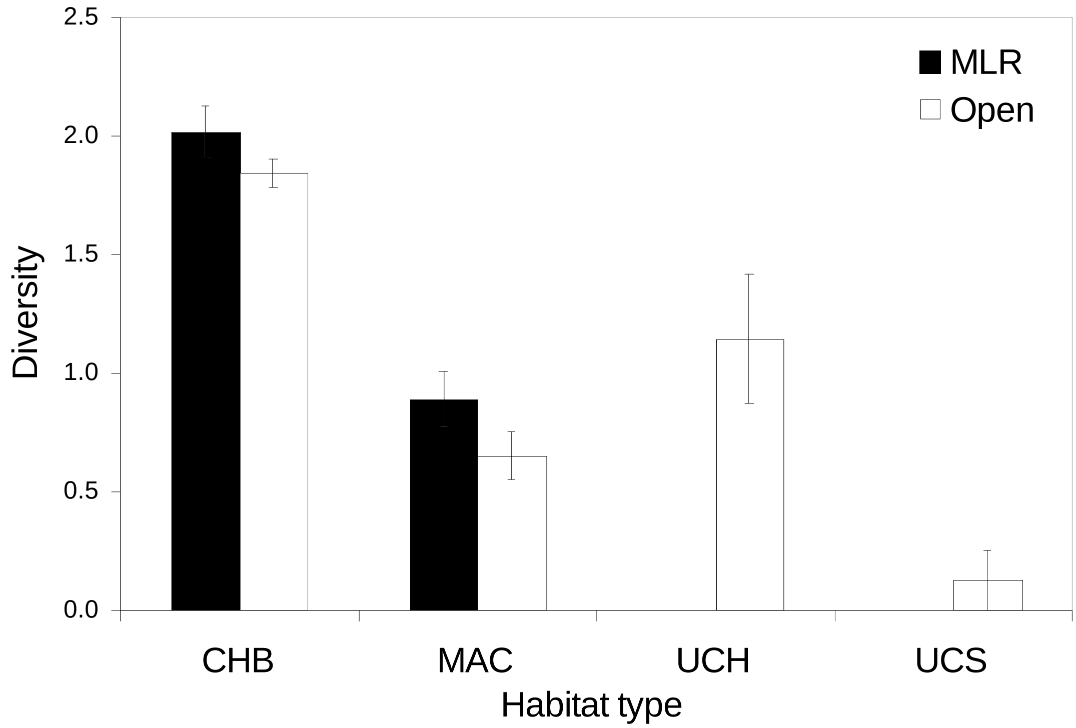

Figure 41. Mean diversity (H’) per transect (125 m^2) by habitat type and management regime for the Kaneohe Bay study area. Error bars are standard error of the mean. MLR = University of Hawaii Marine Laboratory Refuge.

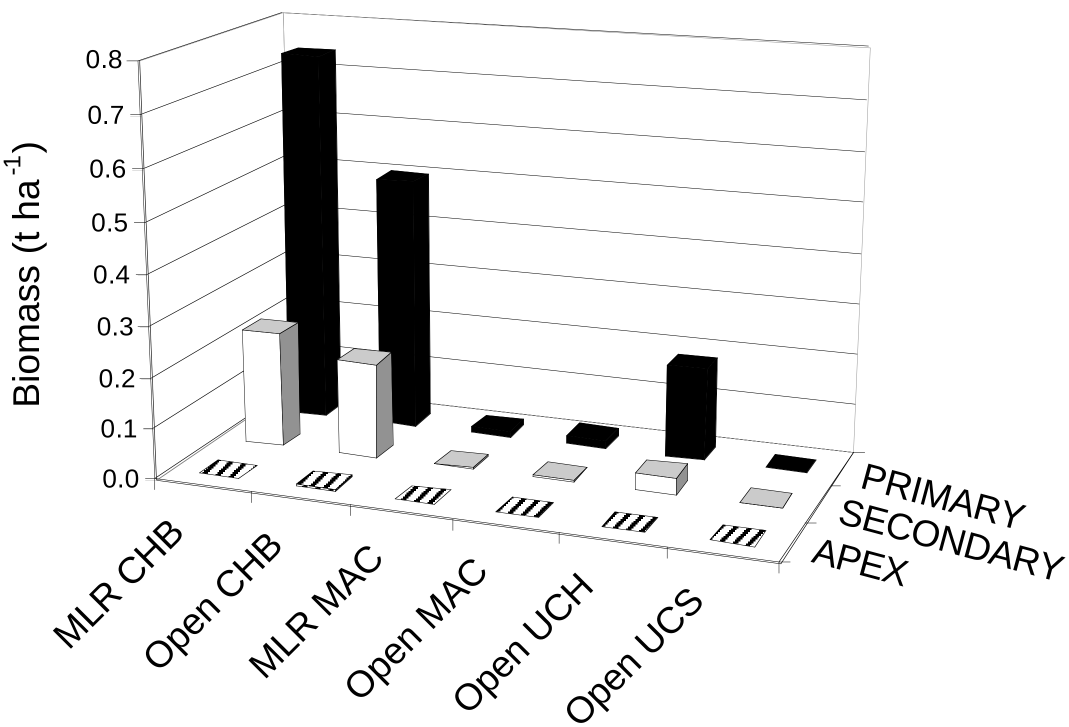

Figure 42. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the Kaneohe Bay study area. MLR = University of Hawaii Marine Laboratory Refuge.

Table 26. Top ten species in the UH Marine Laboratory Refuge, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Chlorurus perspicillatus	Spectacled Parrotfish	*uhu uliuli*	0.25	0.185	60.00	2.11	28.39	1703.51
Scarus sp.	Parrotfish	*uhu*	4.65	0.079	56.67	39.56	12.10	685.57
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	1.02	0.066	60.00	8.70	10.09	605.30
Abudefduf abdominalis	Sargent Major	*mamo*	0.67	0.038	66.67	5.72	5.76	383.81
Scarus psittacus	Palenose Parrotfish	*uhu*	1.25	0.048	50.00	10.61	7.32	366.10
Acanthurus triostegus	Convict Tang	*manini*	0.65	0.041	43.33	5.52	6.26	271.44
Dascyllus albisella	Hawaiian Dascyllus	*aloiloi*	0.52	0.029	50.00	4.45	4.40	219.85
Acanthurus blochii	Ringtail Surgeonfish	*pualu*	0.40	0.021	66.67	3.41	3.26	217.59
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.27	0.021	63.33	2.34	3.22	203.72
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.13	0.015	53.33	1.11	2.36	126.12

Table 27. Top ten species in the Kaneohe Bay open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Scarus psittacus	Palenose Parrotfish	*uhu*	1.49	0.066	40.54	20.25	20.92	847.97
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	1.03	0.056	43.24	14.01	17.76	767.91
Scarus sp.	Parrotfish	*uhu*	2.09	0.050	47.30	28.28	15.71	743.23
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.36	0.012	45.95	4.91	3.91	179.85
Abudefduf abdominalis	Sargent Major	*mamo*	0.42	0.015	25.68	5.76	4.64	119.17
Chlorurus perspicillatus	Spectacled Parrotfish	*uhu uliuli*	0.04	0.024	13.51	0.59	7.42	100.22
Acanthurus triostegus	Convict Tang	*manini*	0.16	0.009	31.08	2.15	2.81	87.35
Acanthurus blochii	Ringtail Surgeonfish	*pualu*	0.19	0.007	31.08	2.61	2.07	64.34
Dascyllus albisella	Hawaiian Dascyllus	*aloiloi*	0.28	0.009	22.97	3.81	2.75	63.18
Mulloidichthys flavolineatus	Yellowstripe Goatfish	*weke*	0.15	0.021	9.46	2.08	6.59	62.30

Honolua-Mokuleia MLCD and west Maui

The west Maui study area extended from Kapalua Bay north to Honolua Bay (ca. 6.2km) and included the Honolua-Mokuleia Bays MLCD.

Sample allocation

A total of 100 samples were collected between July 2 and August 22, 2002 (Fig. 43; Table 28). The two levels of sampling stratification included major habitat types (CHB, SAV, UCH and UCS) and fisheries management regime (open access and MLCD). No macroalgae polygons (minimum mapping unit = one acre) occurred within the MLCD.

Table 28. Sample allocation for west Maui study area.

Habitat	Open	MLCD	Total
Colonized hardbottom	13	15	28
Macroalgae	12		12
Uncolonized hardbottom	23	12	35
Unconsolidated sediment	15	10	25
Total	63	37	100

Large-scale benthic cover

Benthic coverage for the Honolua-Mokuleia MLCD derived from the NOAA benthic habitat maps consisted primarily of sand (45%), followed by uncolonized volcanic rock/boulder (24%), and colonized pavement (18%) (Table 29).

Table 29. Benthic cover for the Honolua-Mokuleia MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized hardbottom	Aggregated coral	12227	6.71
	Colonized pavement	33645	18.47
	Colonized pavement with sand channels	9305	5.11
Sand		82519	45.30
Uncolonized hardbottom	Uncolonized pavement	1167	0.64
	Uncolonized volcanic rock/boulder	43304	23.77
Grand total		182167	100.00

Small-scale benthic cover of substrate types within the management regimes.

The most abundant substrate types in the MLCD were turf algae (41%) and sand/silt (35%) (Table 30; Fig. 44). In comparison, sand (40%) and turf algae cover (38%) were similar in the open access areas. Macroalgae cover was slightly higher in the open access area (13%) than in the MLCD (9%) due to the presence of *Halimeda sp* (3%) in the sand. The most abundant algae (*Melanamansia sp.*), however, was observed at similar levels (3%) in both management strata. Total coral cover was higher in the MLCD (12%) than in the open access area (8%) and was attributed to higher percent cover of *Porites lobata* (5% vs. 4%) in the MLCD. Cover of coralline algae was 4% in the MLCD and 2% in the open access areas. Macorinvertebrates were less than 1% of the benthic cover.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types between the MLCD and the Open areas (Fig. 44). This result indicated that comparing fish assemblages across the management strata was appropriate at the major subtrate types.

Fish assemblage characteristics among habitat types and between management regimes

Fish assemblage characteristics (species richness, biomass, and diversity) were higher in the MLCD compared to the open area over all habitat types (Fig. 45, 46, and 47). The highest values for most assemblage characteristics were found in colonized hardbottom habitat, followed by uncolonized hardbottom, macroalgae, and sand (Fig. 48, 49, and 50; Table 31A, 31B, and 31C). In the three habitat types common to both management strata; richness, biomass, and diversity were all significantly higher ($p<0.05$) in the MLCD (Table 31A, B, and C). Biomass was nearly twice as high in the MLCD compared to open areas.

Fish trophic structure between management regimes and among habitats

Herbivores were the dominant trophic guild by weight over all habitat types, accounting for 61% of the total fish biomass, followed by secondary consumers (36%), and apex predators (3%) (Fig. 51). Although apex predator biomass was low overall, it was 10 times greater in the MLCD compared with the open area.

Species composition by management regime

A number of resource species, primarily surgeonfishes, were important components of the fish assemblage in the MLCD. By biomass, these included: bluespine unicornfish (*kala*, 17%), convict tang (*manini*, 10%), ringtail surgeonfish (*pualu*, *Acanthurus blochii*, 8%), orangespine unicornfish (*umaumalei*, 7%), and whitebar surgeonfish (*maikoiko*, 6%) (Table 32). Other important resource species in the MLCD by total weight included: redlip parrotfish (*palukaluka*, *Scarus rubroviolaceus*, 3%), blue trevally (*omilu*, *Caranx melampygus*, 2.3%), orangeband surgeonfish (*naenae*, *A. olivaceus*, 2.5%), and manybar goatfish (*moana*, *Parupeneus multifasciatus*, 2%). The open area lacked fisheries resource species and was dominated by small surgeonfishes, wrasses, and triggerfishes with little or no resource value (Table 33).

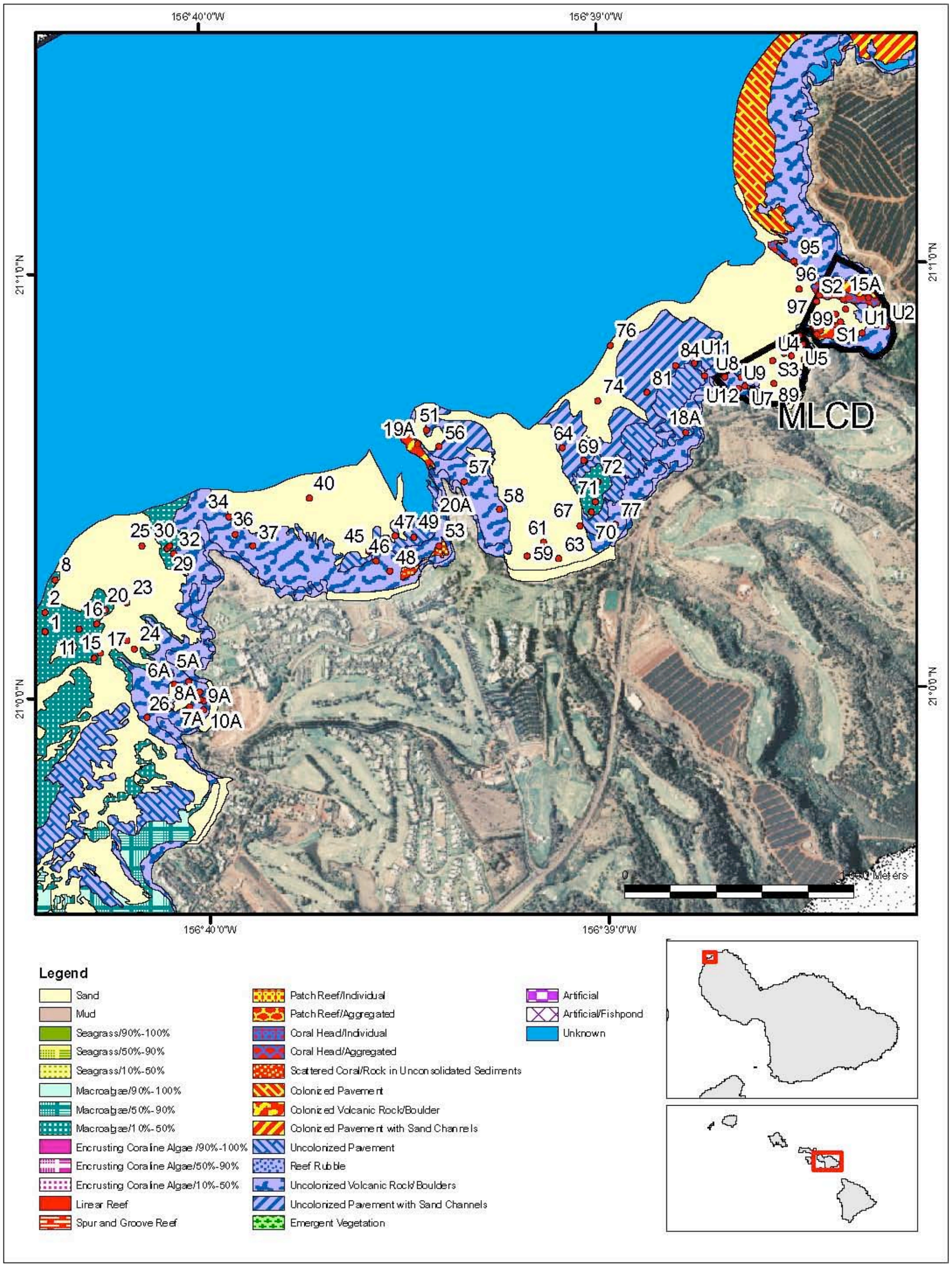

Figure 43. Sampling locations and benthic habitats for the Honolua-Mokuleia MLCD and adjacent areas.

Table 30. Top 10 benthic taxa/substrate types by percent cover within the Honolua Bay and Mokuleia Bay Marine Life Conservation District (MLCD) and the open access area outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		40.8	Sand		39.6
Sand		28.3	Turf algae		38.2
Silt		6.7	Coral	*Porites lobata*	3.5
Coral	*Porites lobata*	4.7	Macroalgae	*Melanamansia sp.*	3.0
Coralline algae		3.5	Macroalgae	*Halimeda sp.*	2.5
Macroalgae	*Melanamansia sp.*	3.1	Coralline algae		1.8
Coral	*Porites compressa*	1.5	Coral	*Montipora capitata*	1.8
Coral	*Montipora capitata*	1.5	Macroalgae	*Microdictyon sp.*	1.4
Macroalgae	*Microdictyon sp.*	1.5	Coral	*Montipora patula*	1.0
Macroalgae	*Dictyosphaeria sp.*	1.4	Macroalgae		0.9

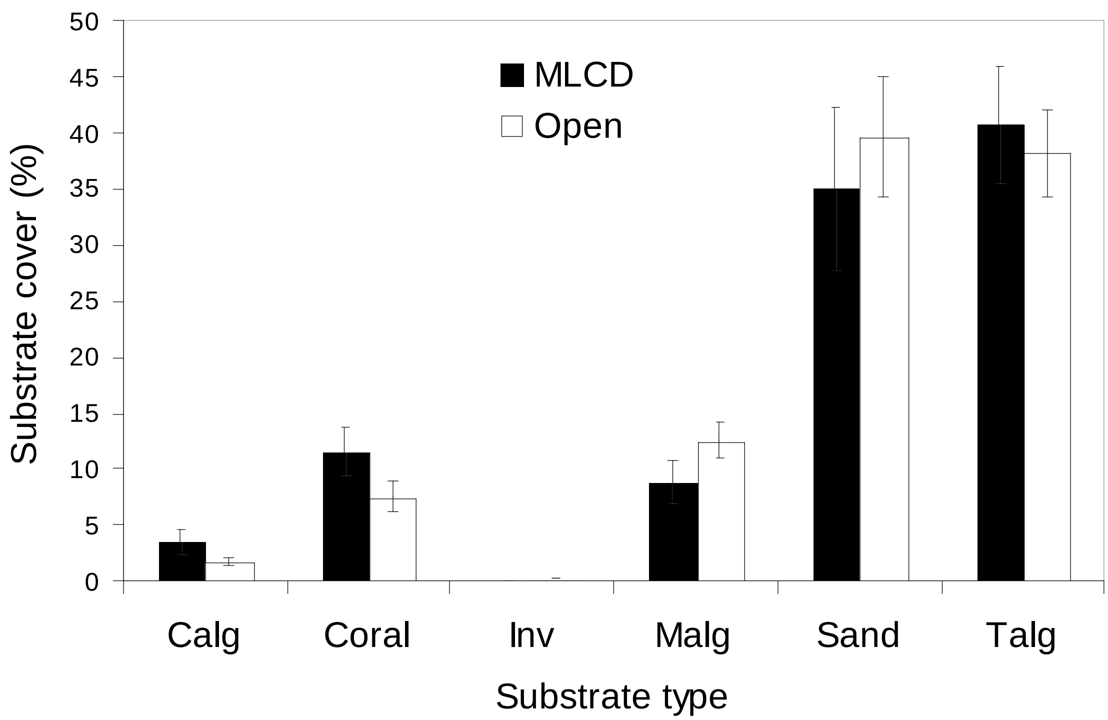

Figure 44. Mean percent cover of substrate types within the Honolua Bay-Mokuleia Marine Life Conservation District (MLCD) and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

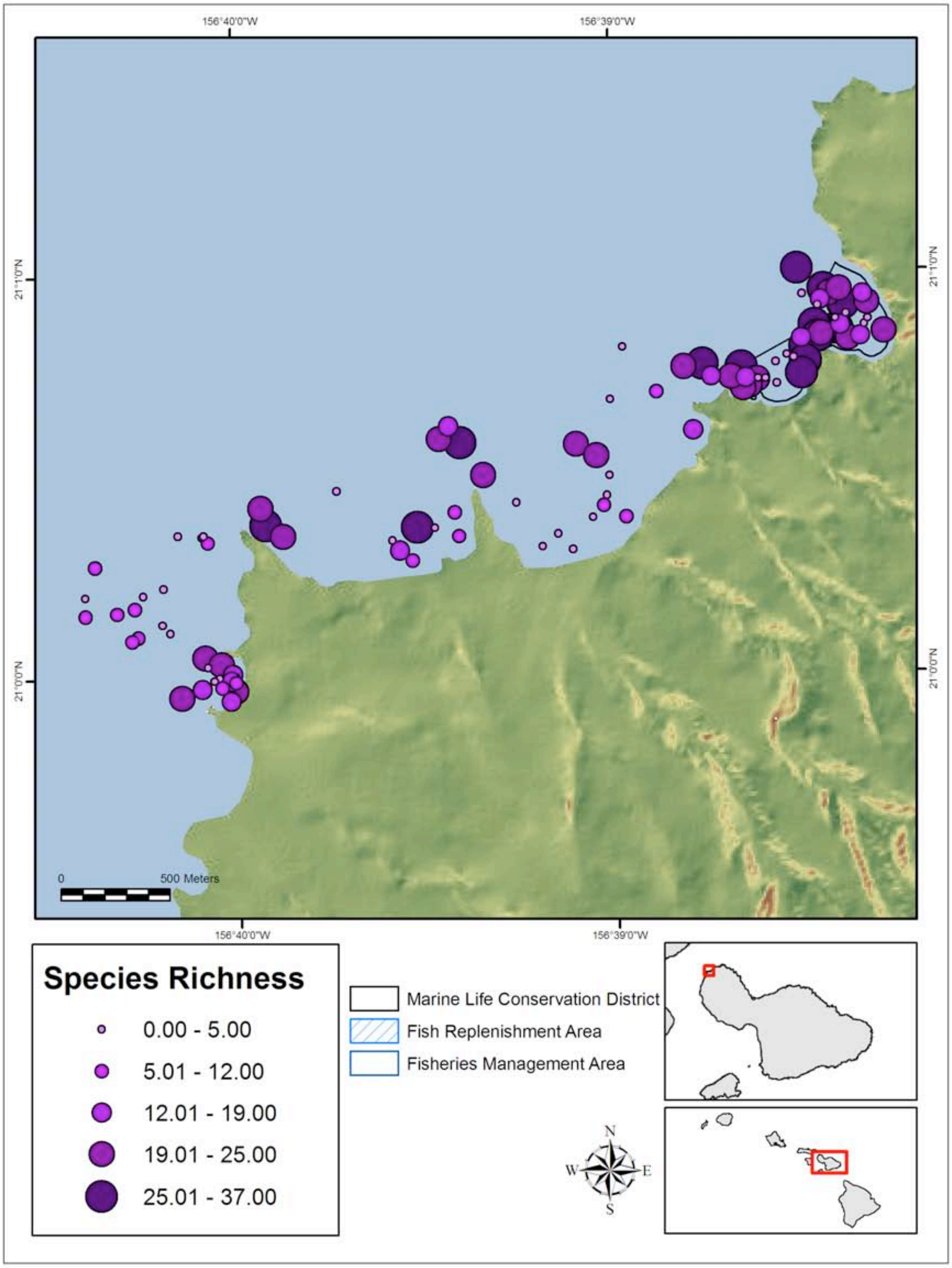

Figure 45. Species richness by individual transects (N=100) for west Maui study area, including Honolua-Mokuleia MLCD. Classification based on quantiles.

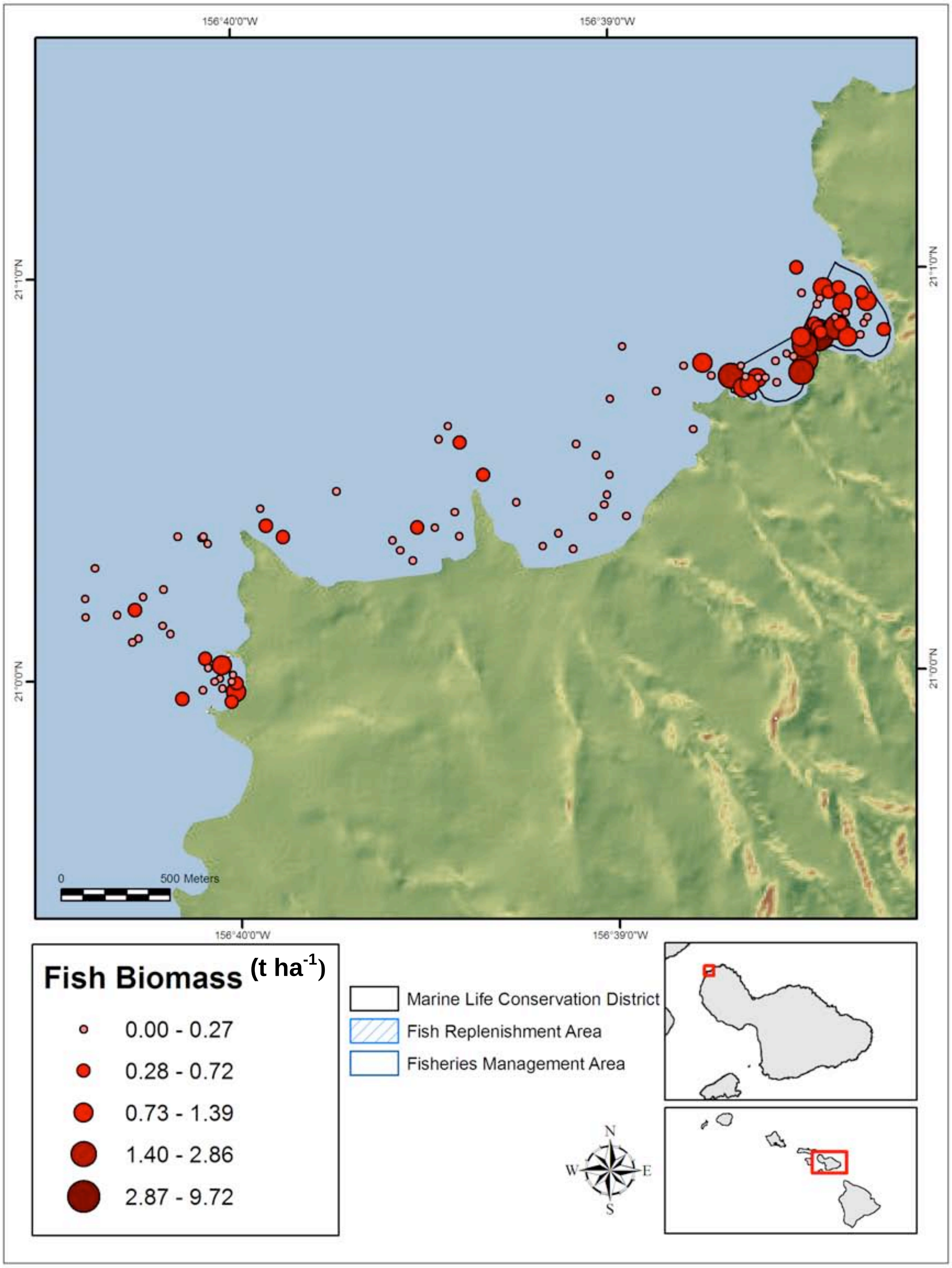

Figure 46. Fish biomass (t ha^{-1}) by individual transects (N=100) for west Maui study area, including Honolua-Mokuleia MLCD. Classification based on quantiles.

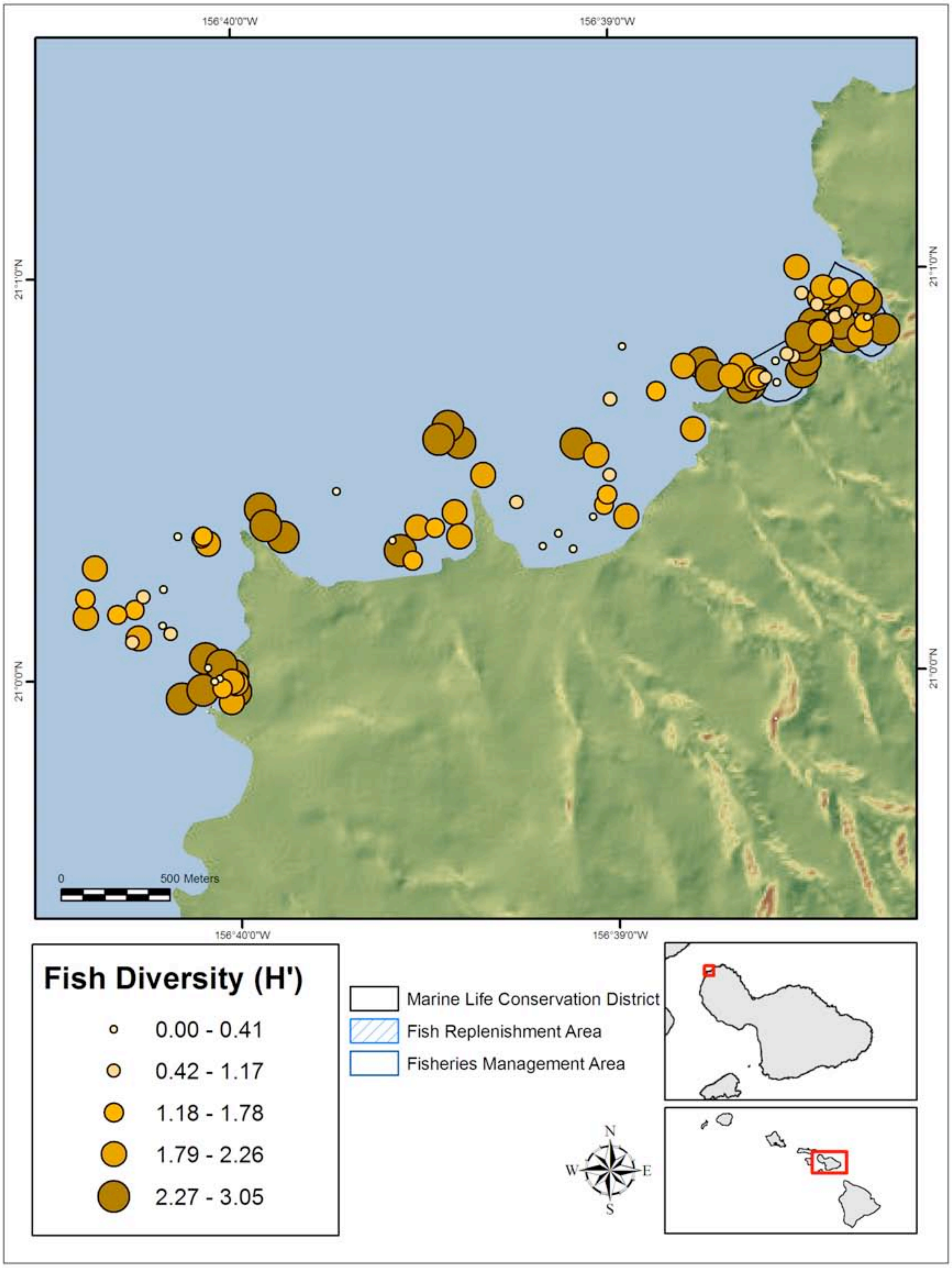

Figure 47. Fish diversity (H') by individual transects (N=100) for west Maui study area, including Honolua-Mokuleia MLCD. Classification based on quantiles.

Table 31A. Comparison of fish species richness among management regimes and habitat types for the west Maui study area. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 88). Management regimes: MLCD ([M]); Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB); <10% live coral hard bottom (UCH); and unconsolidated sediments (UCS). Unplanned multiple comparisons among management strata and habitat$_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different (α = 0.05)

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	1367	41.7	<0.001	
Management	1	277	8.5	0.005	MLCD > Open
Habitat$_{[management]}$	4	1573	48.0	<0.001	
Error	82	33			
Habitat$_{[management]}$ -					$\text{CHB}_{[M]}$ $\text{CHB}_{[O]}$ $\text{UCH}_{[M]}$ $\text{UCH}_{[O]}$ $\text{UCS}_{[M]}$ $\text{UCS}_{[O]}$

Table 31B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the west Maui study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	0.96	19.5	<0.0001	
Management	1	1.17	24.0	<0.0001	MLCD > Open
Habitat$_{[management]}$	4	0.76	15.6	<0.0001	
Error	82	0.05			
Habitat$_{[management]}$ -					$\text{CHB}_{[M]}$ $\text{UCH}_{[M]}$ $\text{CHB}_{[O]}$ $\text{UCH}_{O]}$ $\text{UCS}_{[M]}$ $\text{UCS}_{[O]}$

Table 31C. Comparison of fish species diversity (H') among management regimes and habitat types for the west Maui study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	13.1	92.3	<0.001	
Management	1	1.6	11.0	0.001	MLCD > Open
Habitat$_{[management]}$	4	15.8	111.4	<0.001	
Error	82	0.9			
Habitat$_{[management]}$ -					$\text{UCH}_{[M]}$ $\text{CHB}_{[M]}$ $\text{CHB}_{[O]}$ $\text{UCH}_{[O]}$ $\text{UCS}_{[M]}$ $\text{UCS}_{[O]}$

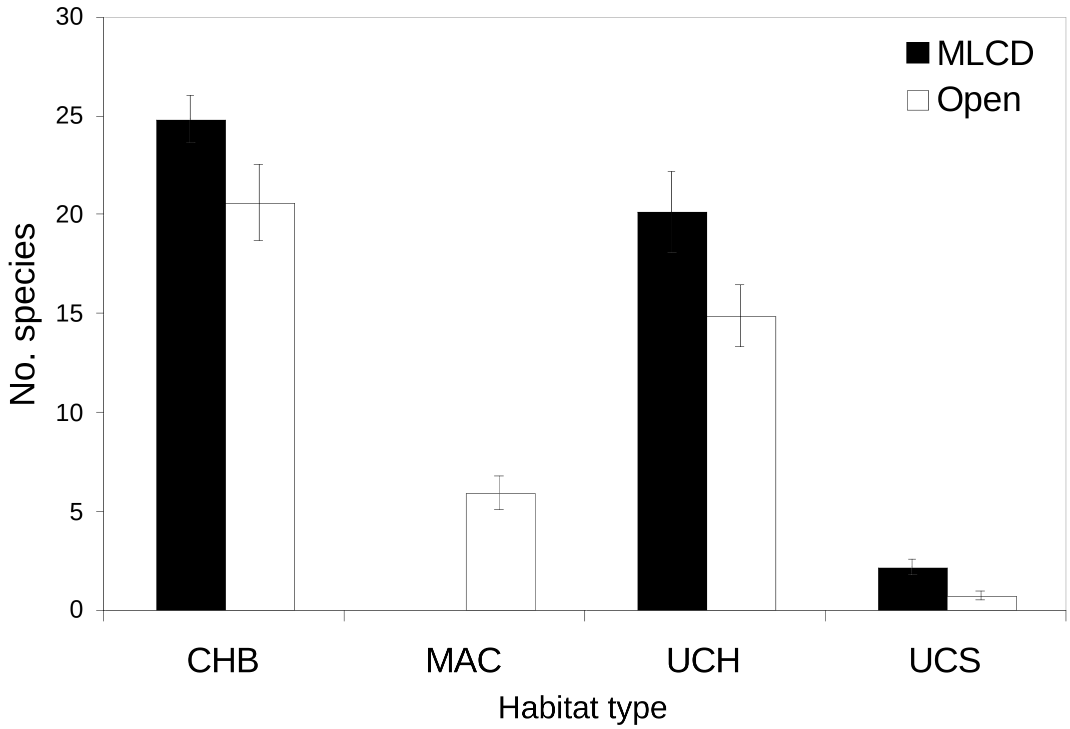

Figure 48. Mean number of species per transect (125 m^2) by habitat type and management regime for the west Maui study area. Error bars are standard error of the mean.

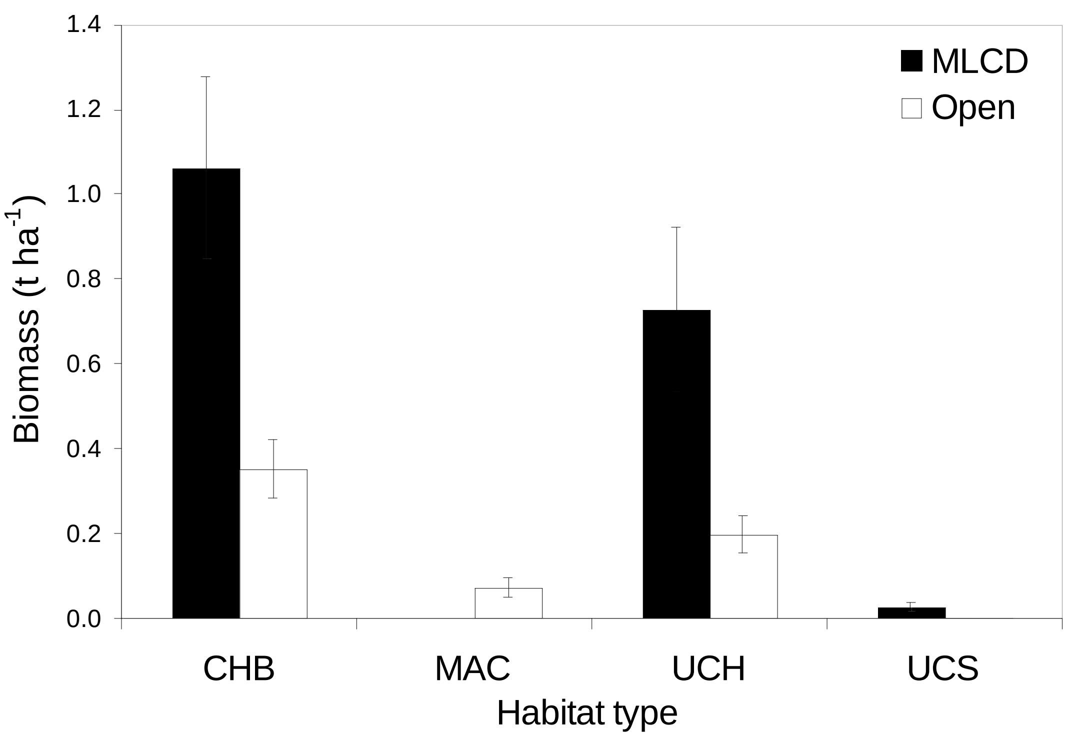

Figure 49. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the west Maui study area. Error bars are standard error of the mean.

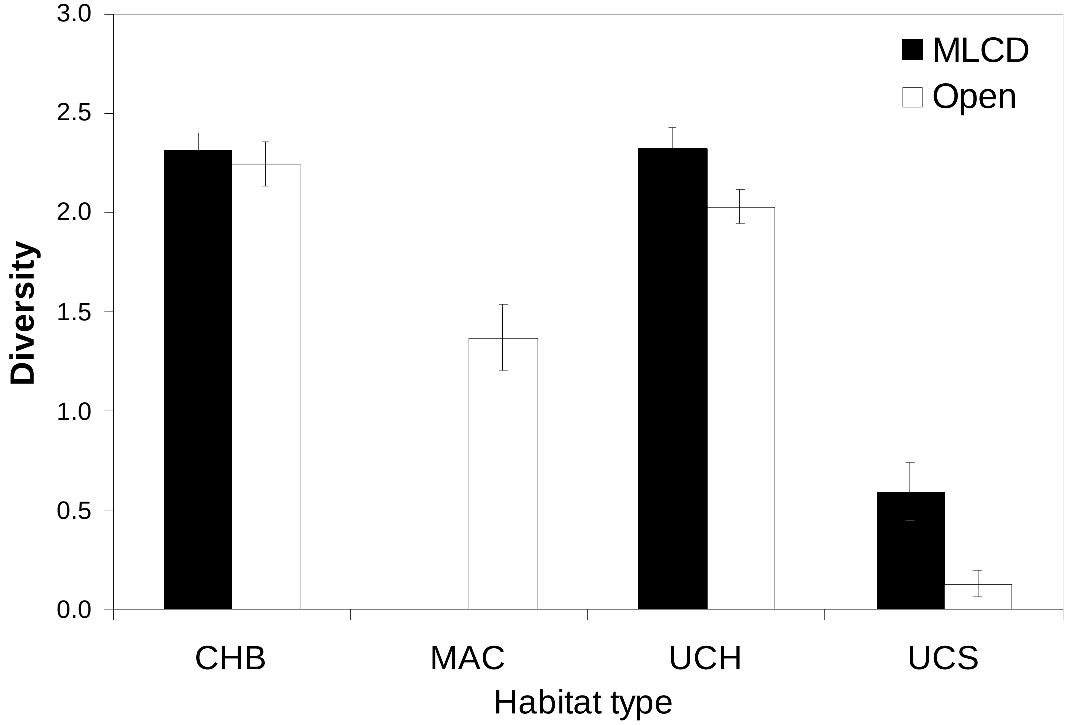

Figure 50. Mean diversity (H’) per transect (125 m^2) by habitat type and management regime for the west Maui study area. Error bars are standard error of the mean.

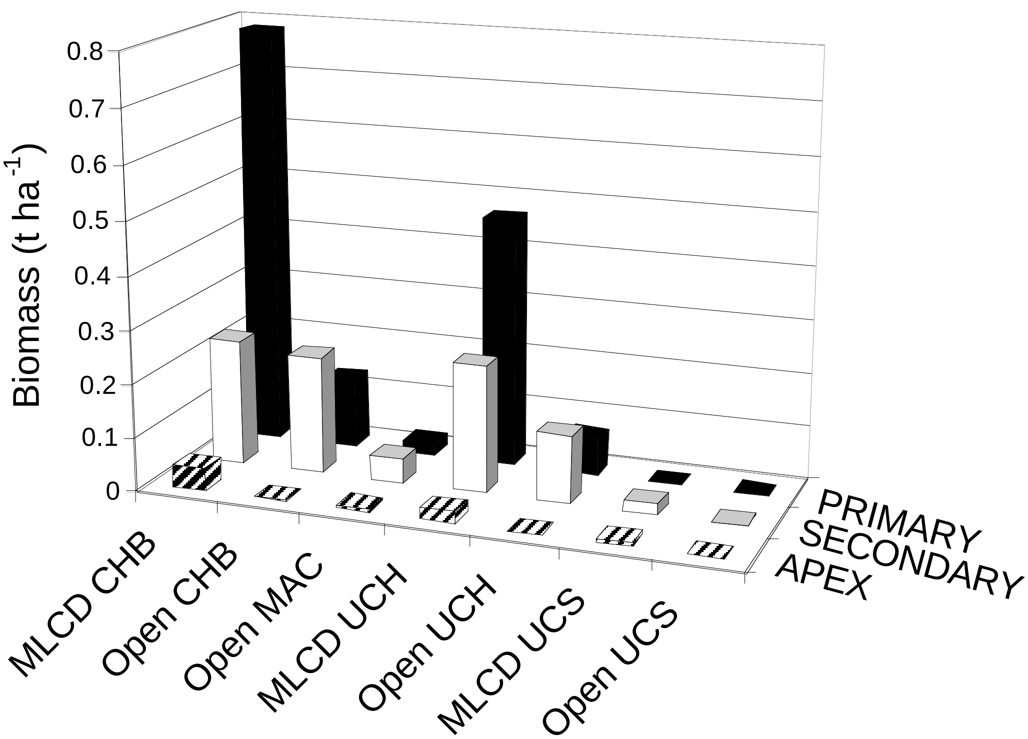

Figure 51. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the west Maui study area.

Table 32. Top ten species in the Honolua-Mokuleia MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Naso unicornis	Bluespine Unicornfish	*kala*	0.14	0.115	37.84	1.61	17.05	645.20
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	1.04	0.047	67.57	11.70	6.94	468.78
Acanthurus triostegus	Convict Tang	*manini*	0.54	0.071	29.73	6.13	10.48	311.58
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.12	0.044	40.54	1.31	6.55	265.42
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.17	0.042	35.14	1.95	6.23	218.94
Acanthurus blochii	Ringtail Surgeonfish	*pualu*	0.13	0.053	24.32	1.41	7.79	189.55
Scarus rubroviolaceus	Redlip Parrotfish	*palukaluka*	0.16	0.019	40.54	1.85	2.86	116.09
Parupeneus multifasciatus	Manybar Goatfish	*moano*	0.16	0.013	56.76	1.78	1.95	110.83
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.06	0.017	29.73	0.63	2.48	73.82
Caranx melampygus	Blue Trevally	*omilu*	0.03	0.016	29.73	0.34	2.34	69.68

Table 33. Top ten species in the west Maui open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.51	0.020	44.44	10.87	12.48	554.8642
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.55	0.009	44.44	11.79	5.47	243.2627
Rhinecanthus rectangulus	Reef Triggerfish	*humuhumunukunukuapuaa*	0.07	0.009	41.27	1.50	5.36	221.3795
Sufflamen fraenatus	Bridled Triggerfish	*humuhumumimi*	0.03	0.012	25.40	0.55	7.80	198.0132
Parupeneus multifasciatus	Manybar Goatfish	*moano*	0.12	0.008	38.10	2.48	4.86	185.0386
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.05	0.007	26.98	1.17	4.17	112.5521
Stethojulis balteata	Belted Wrasse	*omaka*	0.27	0.002	44.44	5.81	1.36	60.65415
Mulloidichthys flavolineatus	Yellowstripe Goatfish	*weke*	0.12	0.012	7.94	2.54	7.35	58.30423
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.02	0.005	12.70	0.46	3.46	43.89139
Bodianus bilunulatus	Hawaiian Hogfish	*aawa*	0.03	0.003	22.22	0.60	1.94	43.12856

Molokini Shoal MLCD and south Maui
The study area included the Molokini Shoal MLCD and the Makena and Keawakapu areas of south Maui (ca. 8.2km).

Sample allocation

A total of 70 samples were collected between October 25 and December 22, 2004 (Fig. 52A, 52B, and 52C; Table 34). The two levels of sampling stratification included major habitat types (CHB, UCH and UCS) and fisheries management regime (open access and MLCD). Because there was no habitat adjacent to the Molokini Shoal MLCD, two areas along the south Maui coast (Keawakapu and Makena) were selected as control areas based on similar habitat features, wave exposure, and proximity to the MLCD.

Table 34. Sample allocation for Molokini Shoal and south Maui study area.

Habitat	MLCD	Open	Total
Colonized hardbottom	23	15	38
Uncolonized hardbottom	-	2	2
Unconsolidated sediment	15	15	30
Total	38	32	70

Large-scale benthic cover

No benthic habitat maps have been developed at Molokini to date.

Small-scale benthic cover of substrate types within the management regimes.

In the MLCD, the most abundant substrate types were turf algae (41%) and sand (29%) (Table 35; Fig. 53). In the open access areas, sand (44%) was the most prevalent substrate followed by turf algae cover (26%). Average coral cover was quite high in the MLCD (28%) and the open access area (22%). In the MLCD, the predominant corals were *Montipora patula* (9%), *Porites lobata* (8%), *M. capitata* (6%), and *Pocillopora meandrina* (5%). Similar species were documented in the open access area, but coverage was different with *P. lobata* (10%), *Porites compressa* (4%), *M. patula* (4%), and *M. capitata* (3%) rounding out the top four. Little macroalgae was observed in Molokini (<1%) compared to 8% cover in the open access area. *Cladophora sp.* (2%), Cyanobacteria (2%), *Halimeda sp* (1%), and *Tolypiocladia sp.* (1%) were the predominant algal types. Both coralline algae cover (<1.5%) and abundance of macorinvertebrates were low (<1%) in the two management strata.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types between the MLCD and the open areas (Fig. 53). This result indicated that comparing fish assemblages across the management strata was appropriate at the major subtrate types.

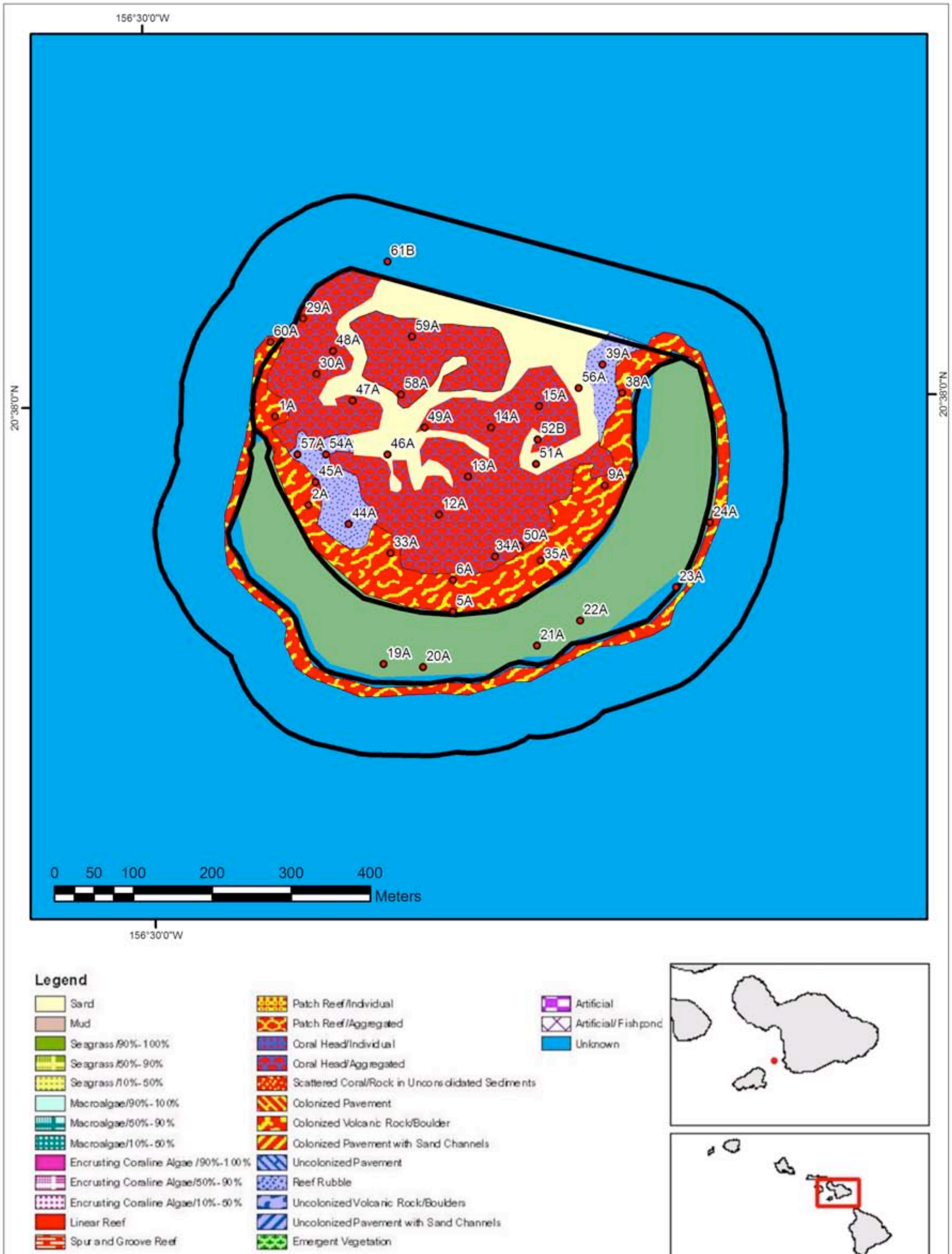

Figure 52A. Sampling locations and benthic habitats for the Molokini Shoals MLCD.

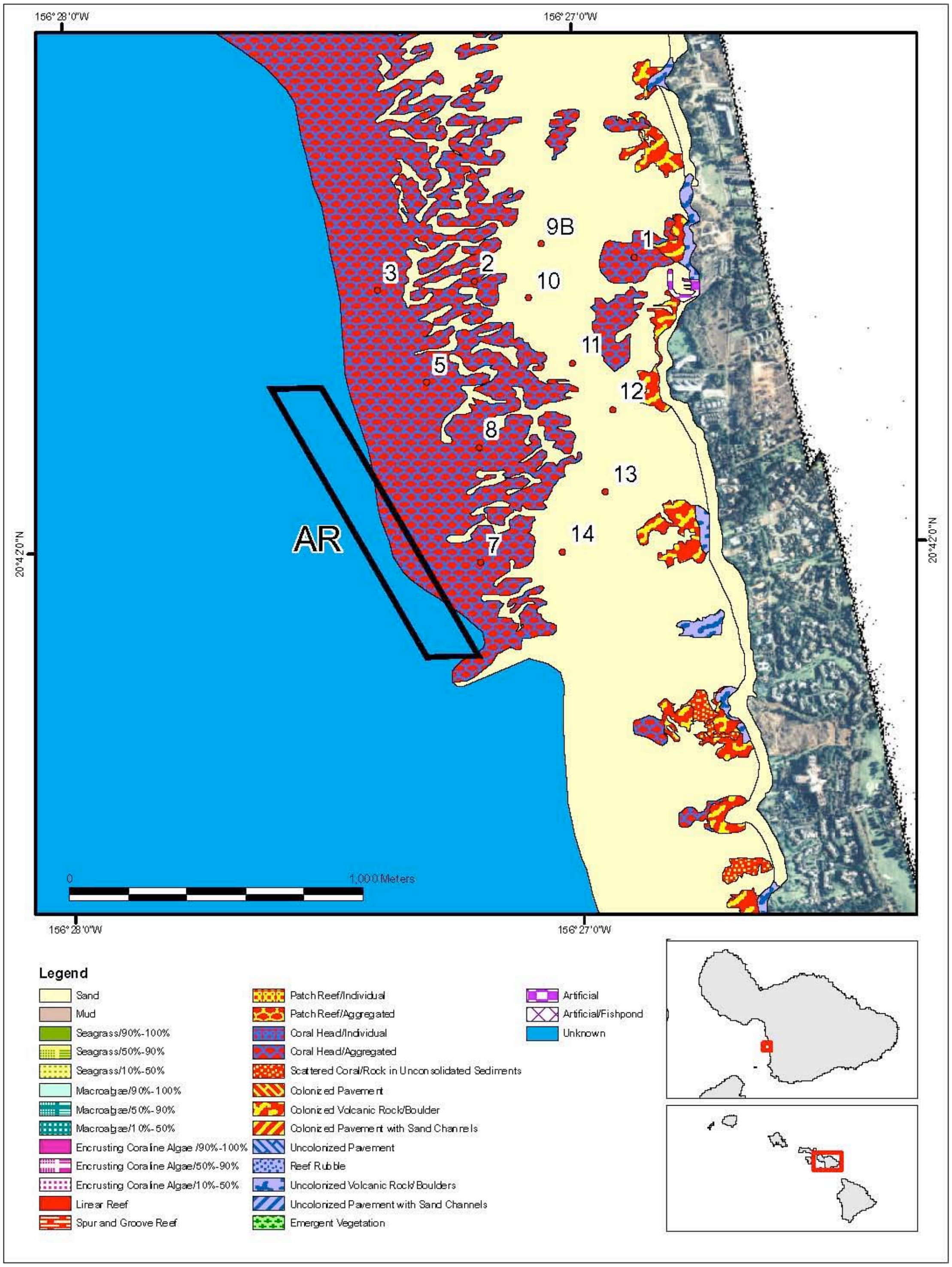

Figure 52B. Sampling locations and benthic habitats for the Keawakapu, south Maui study area. AR = location of artifical reef permit area.

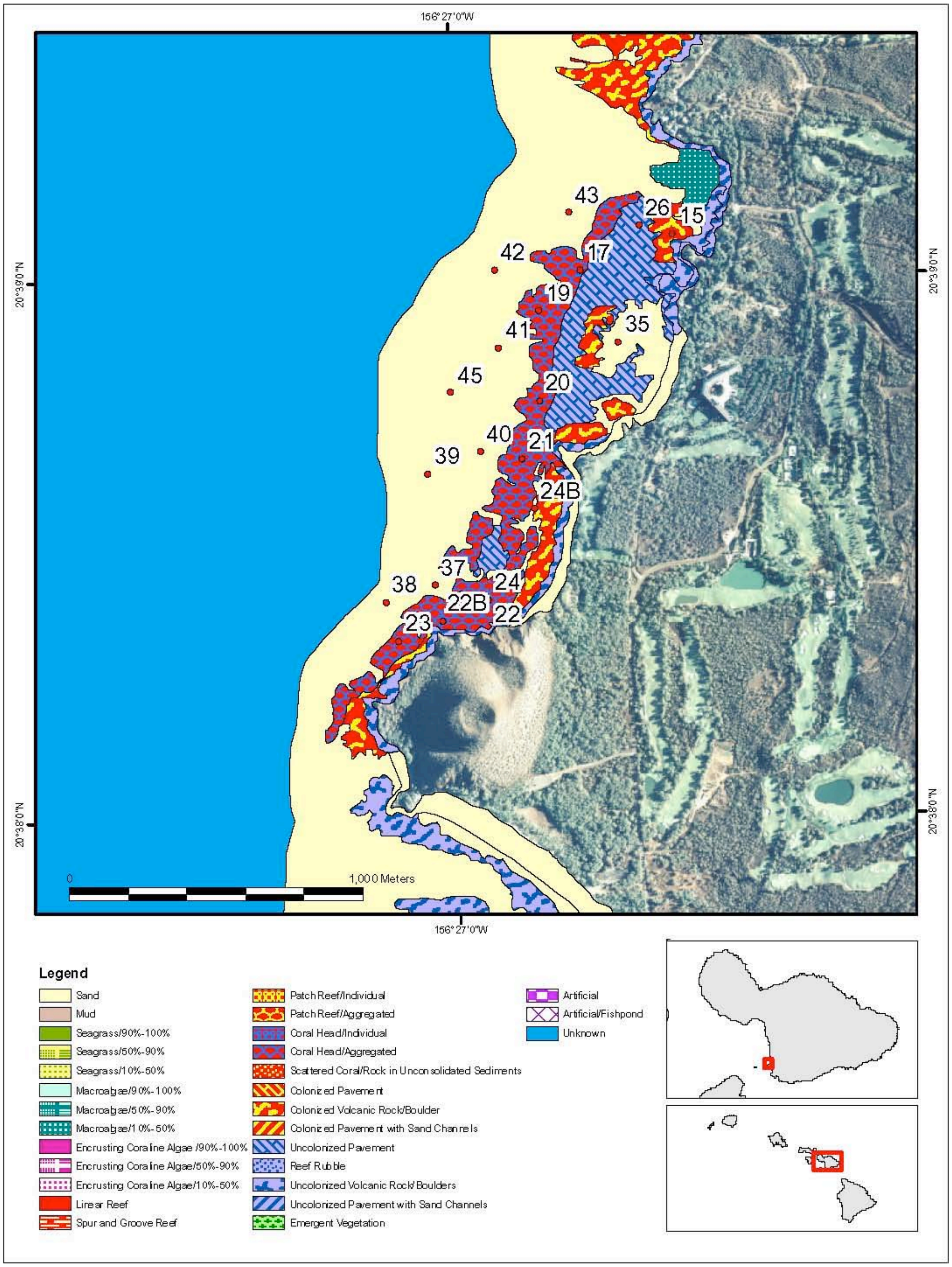

Figure 52C. Sampling locations and benthic habitats for the Makena, south Maui study area.

Table 35. Top 10 benthic taxa/substrate types by percent cover within the Molokini Marine Life Conservation District (MLCD) and the open access area outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		40.6	Sand		43.8
Sand		28.7	Turf algae		25.9
Coral	*Montipora patula*	9.1	Coral	*Porites lobata*	9.5
Coral	*Porites lobata*	7.7	Coral	*Porites compressa*	3.8
Coral	*Montipora capitata*	6.0	Coral	*Montipora patula*	3.6
Coral	*Pocillopora meandrina*	4.8	Coral	*Montipora capitata*	3.3
Coralline algae		1.2	Macroalgae	*Cladophora sp.*	2.3
Coral	*Porites compressa*	0.3	Macroalgae	*Cyanobacteria*	2.2
Macroinvertebrate	*Clathria sp.*	0.3	Macroalgae	*Halimeda sp.*	1.4
Coral	*Pavona varians*	0.2	Macroalgae	*Tolypiocladia sp.*	0.9

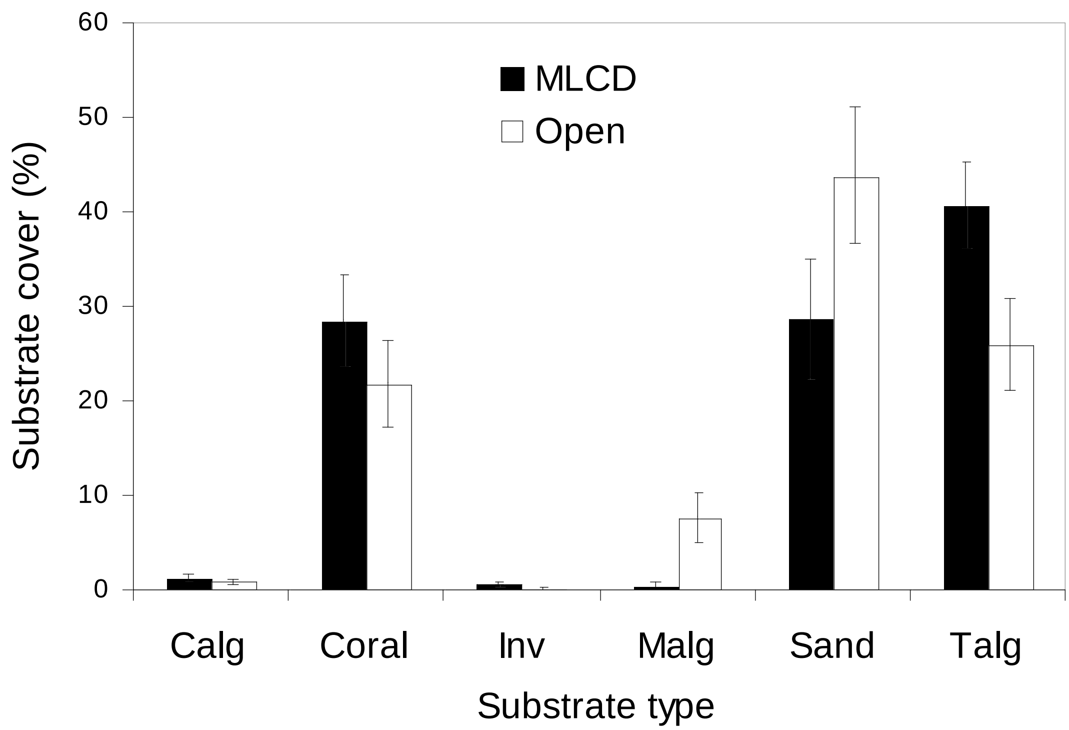

Figure 53. Mean percent cover of substrate types within the Molokini Marine Life Conservation District (MLCD) and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

Fish assemblage characteristics among habitat types and between management regimes

The Molokini Shoal MLCD had higher values for most fish assemblage characteristics compared to similar open areas along the south Maui coast (Fig. 54A, 54B; 55A, 55B, 56A, and 56B). Species richness (Fig. 57) and biomass (Fig. 58) were higher in the colonized hardbottom habitat, while diversity was similar between colonized and uncolonized habitat types (Fig. 59). Within the two habitat types common to the MLCD and open areas (colonized hardbottom and sand), species richness, biomass, and diversity were all significantly higher in the MLCD (Table 36A, 36B, and 36C). Colonized hardbottom had higher values for richness and diversity, regardless of management regime, but sand habitat within the MLCD harbored higher biomass than the colonized hardbottom habitat in the areas open to fishing.

Fish trophic structure between management regimes and among habitats

There were dramatic differences in fish trophic structure between the MLCD and open areas (Fig. 60). In the MLCD, herbivores accounted for 42% of total fish biomass, followed by apex predators (41%), and secondary consumers (17%). This large proportion of apex predators was comprised primarily of sharks and jacks. In contrast, apex predators accounted for only 5% of fish biomass in the open areas.

Species composition by management regime

The dominant species in the MLCD included a mix of surgeonfishes, triggerfishes, sharks, jacks, and parrotfishes (Table 37). This diverse assemblage included a number of important resource species, such as blue trevally (*omilu*), giant trevally (*ulua*, *Caranx ignobilis*), and bigeye emperor (*mu*, *Monotaxis grandoculis*). In comparison, small surgeonfishes and wrasses dominated the open access areas (Table 38). The few resource species in the open area included goldring surgeonfish (*kole*), parrotfish (*uhu*), and orangespine unicornfish (*umaumalei*).

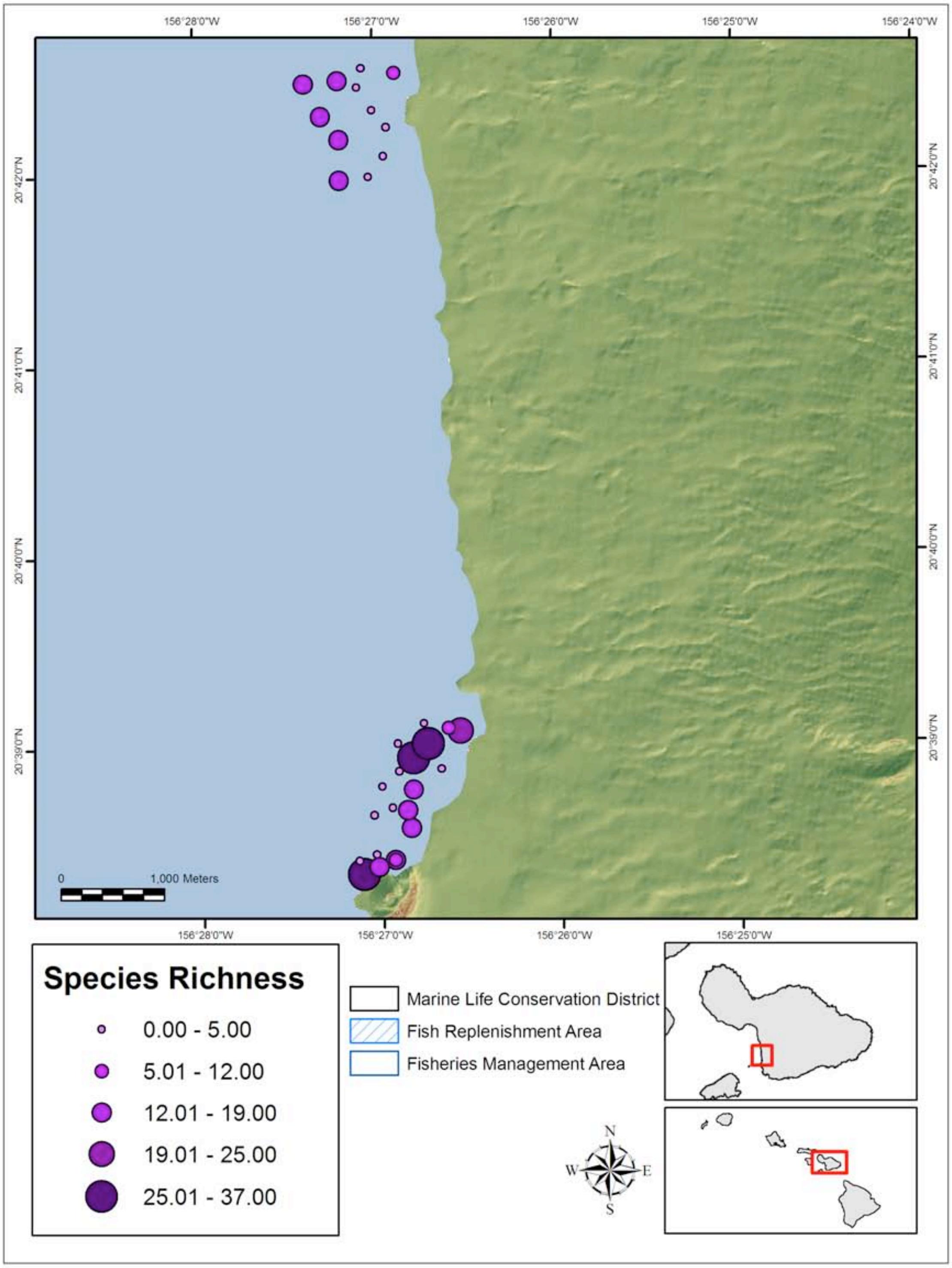

Figure 54A. Species richness by individual transects (N=70) for south Maui study area. Classification based on quantiles.

Figure 54B. Species richness by individual transects (N=38) for Molokini Shoal MLCD. Classification based on quantiles.

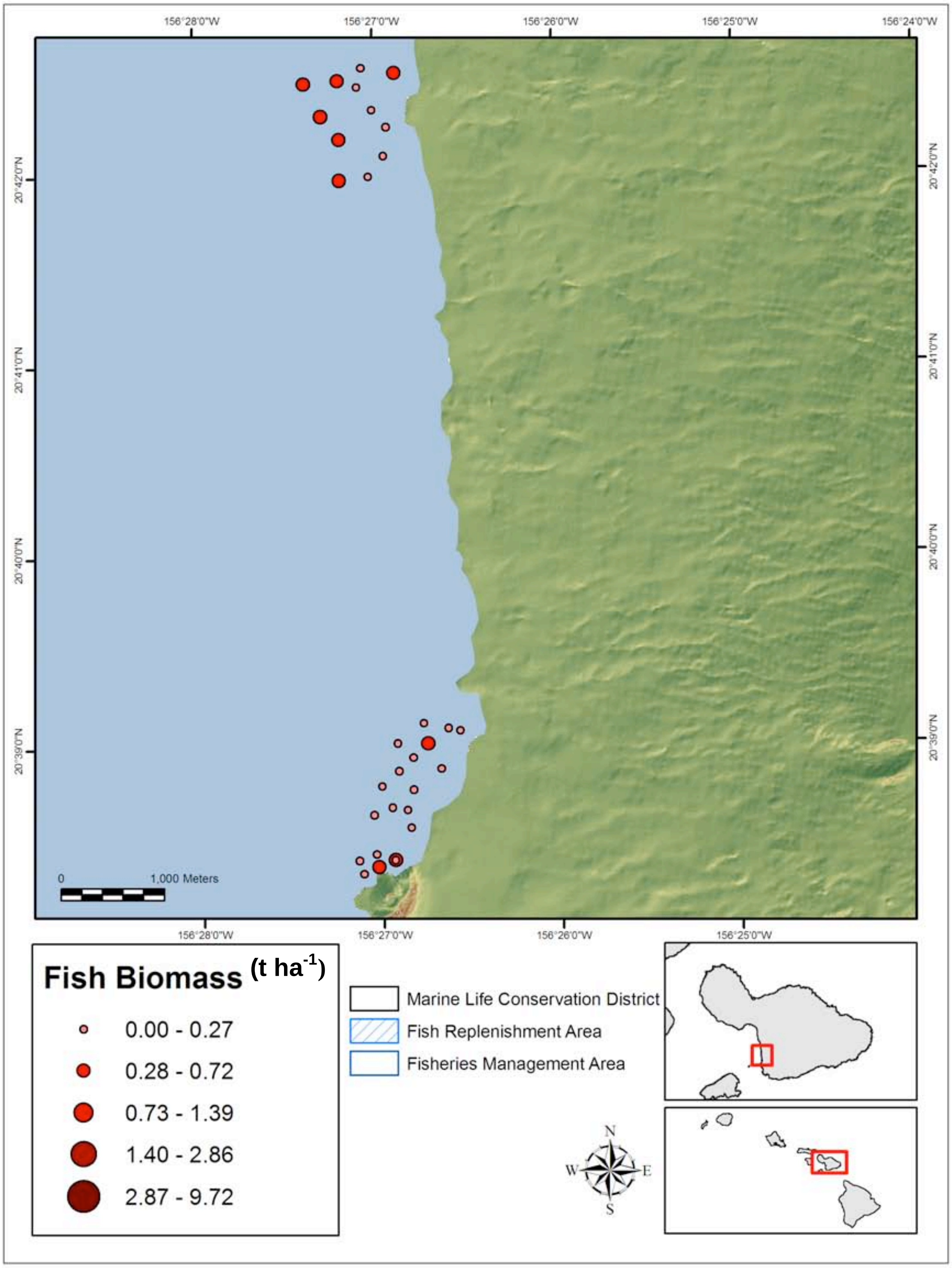

Figure 55A. Fish biomass (t ha^{-1}) by individual transects (N=70) for south Maui study area. Classification based on quantiles.

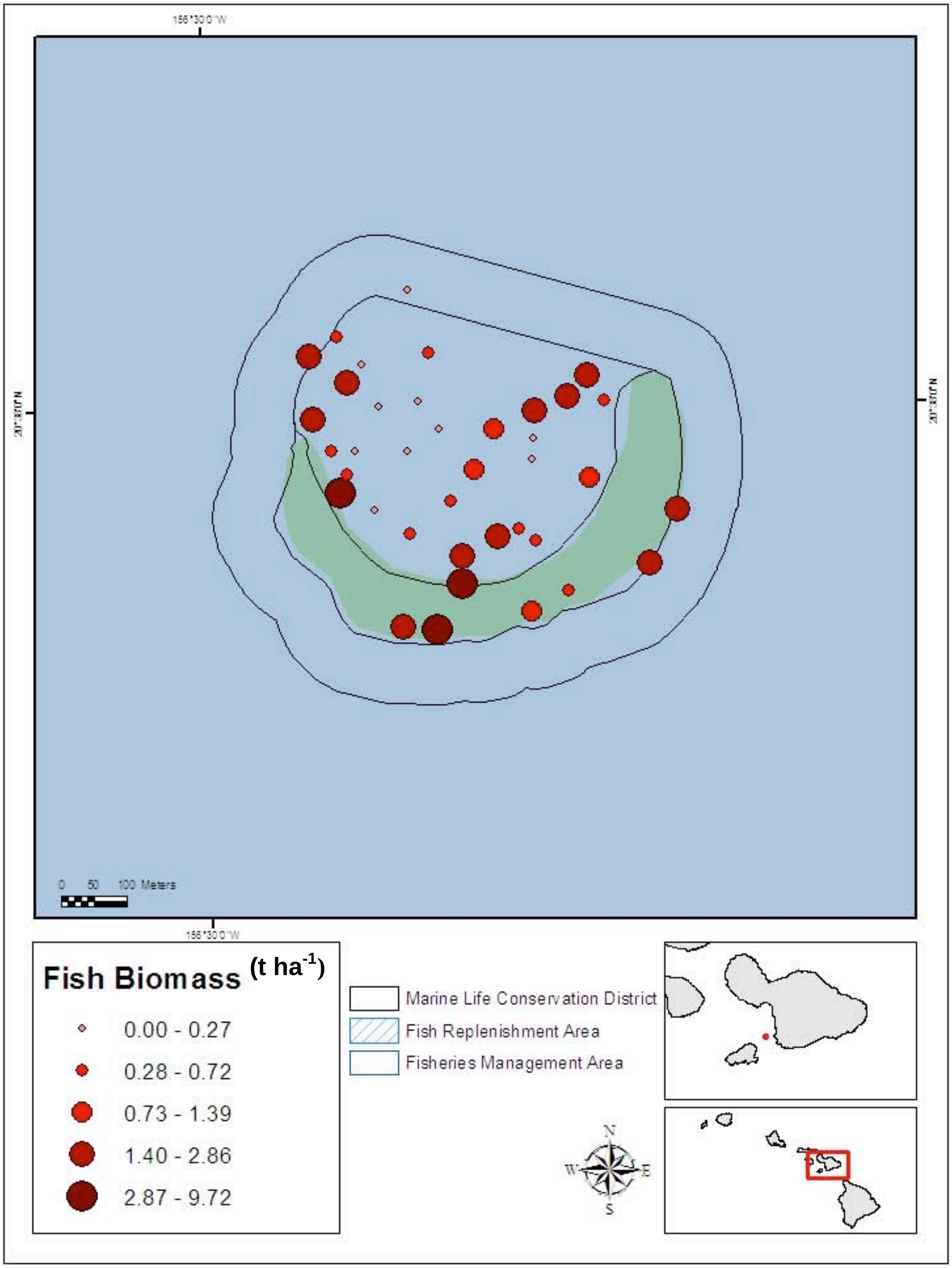

Figure 55B. Fish biomass (t ha^{-1}) by individual transects (N=38) for Molokini Shoal MLCD. Classification based on quantiles.

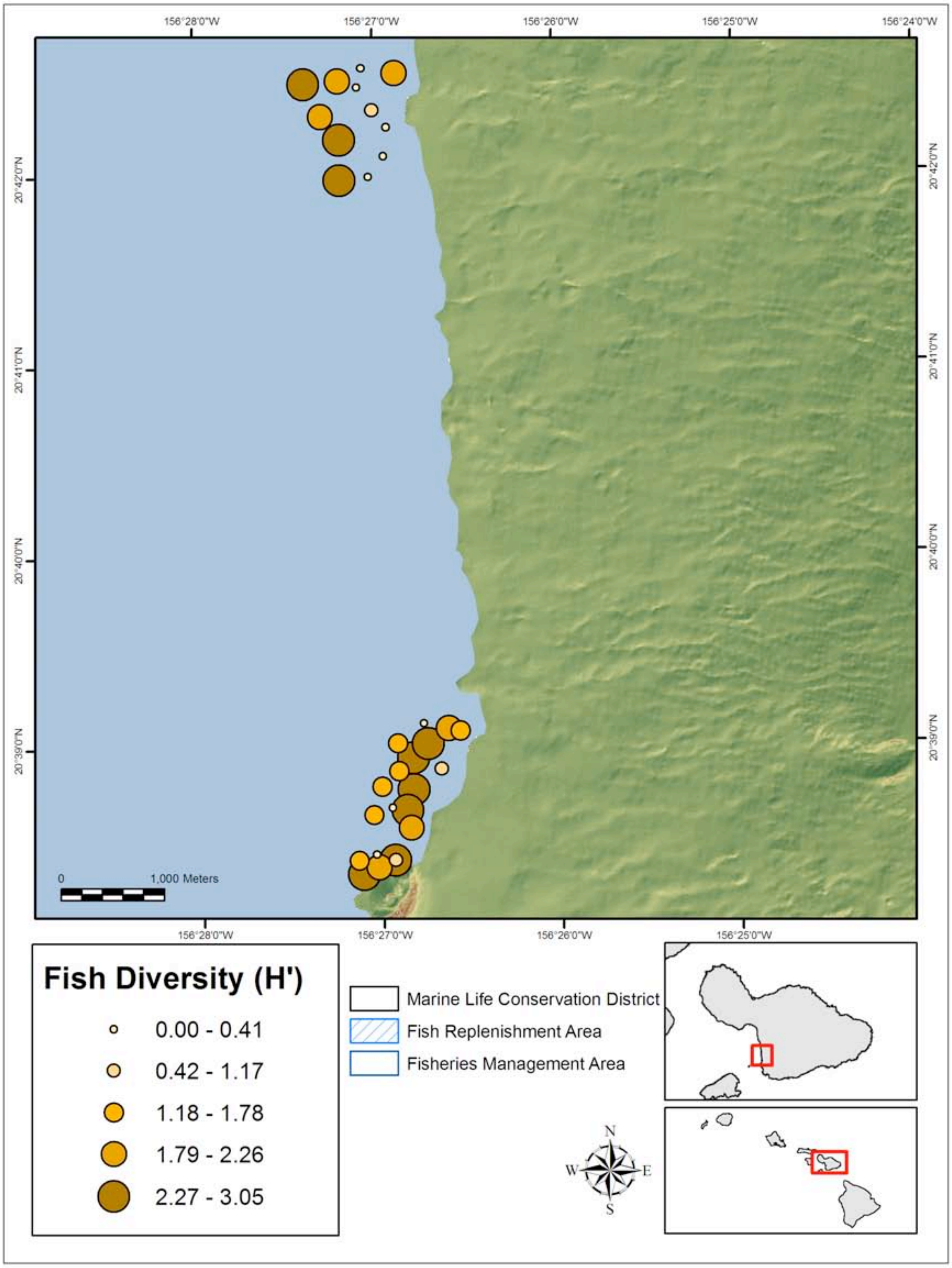

Figure 56A. Fish diversity (H') by individual transects (N=70) for south Maui study area including Molokini Shoal MLCD. Classification based on quantiles.

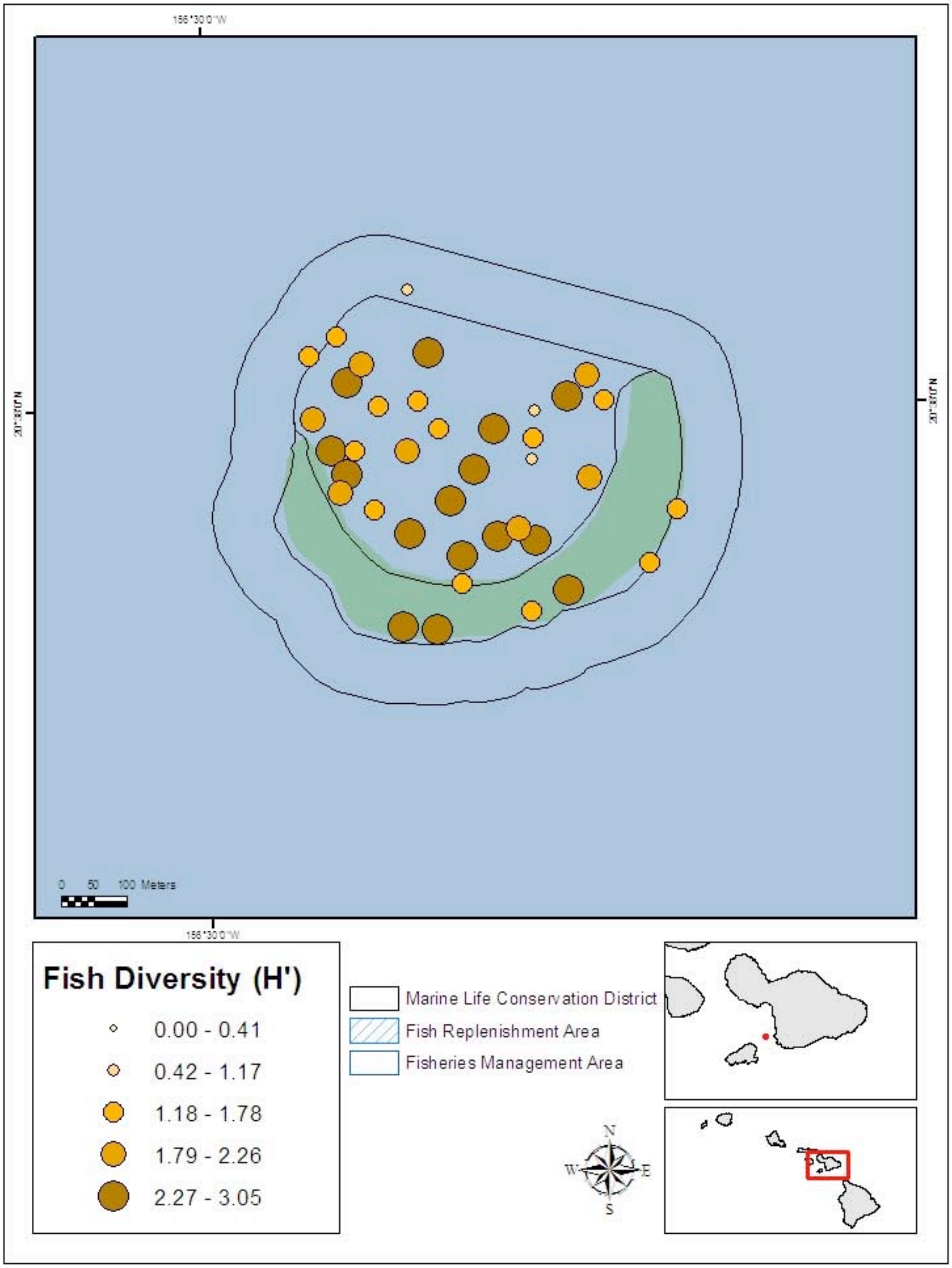

Figure 56B. Fish diversity (H') by individual transects (N=38) for Molokini Shoal MLCD. Classification based on quantiles.

Table 36A. Comparison of fish species richness among management regimes and habitat types for the south Maui and Molokini Shoal study area. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 68). Management regimes: MLCD ([M]) and Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB) and unconsolidated sediments (UCS). Unplanned multiple comparisons among management strata and $\text{habitat}_{[\text{management}]}$ tested using Tukey's HSD tests. Underlined means are not significantly different (α = 0.05)

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	1414	70.0	<0.001	
Management	1	411	20.3	<0.001	MLCD > Open
$\text{Habitat}_{[\text{management}]}$	2	1764	87.3	<0.001	
Error	64	20			
$\text{Habitat}_{[\text{management}]}$ -					$\text{CHB}_{[M]}$ $\text{CHB}_{[O]}$ $\text{UCS}_{[M]}$ $\text{UCS}_{[O]}$

Table 36B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the south Maui and Molokini Shoal study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	2.8	26.2	<0.0001	
Management	1	3.2	30.5	<0.0001	MLCD > Open
$\text{Habitat}_{[\text{management}]}$	2	2.0	18.8	<0.0001	
Error	64	0.1			
$\text{Habitat}_{[\text{management}]}$ -					$\text{CHB}_{[M]}$ $\underline{\text{UCS}_{[M]}\ \ \text{CHB}_{[O]}\ \ \text{UCS}_{[O]}}$

Table 36C. Comparison of fish species diversity (H') among management regimes and habitat types for the south Maui and Molokini Shoal study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	9.5	31.9	<0.001	
Management	1	4.2	14.2	<0.001	MLCD > Open
$\text{Habitat}_{[\text{management}]}$	2	12.5	38.7	<0.001	
Error	64	0.5			
$\text{Habitat}_{[\text{management}]}$ -					$\underline{\text{CHB}_{[O]}\ \ \text{CHB}_{[M]}}$ $\text{UCS}_{[M]}$ $\text{UCS}_{[O]}$

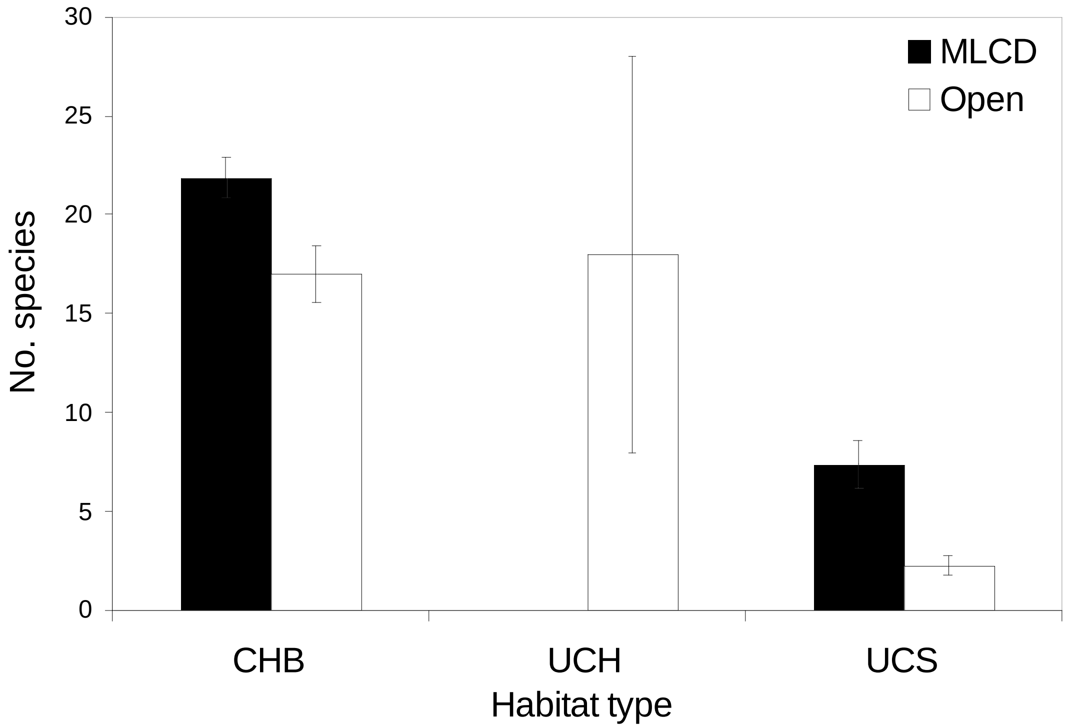

Figure 57. Mean number of species per transect (125 m^2) by habitat type and management regime for the south Maui and Molokini Shoal study area. Error bars are standard error of the mean.

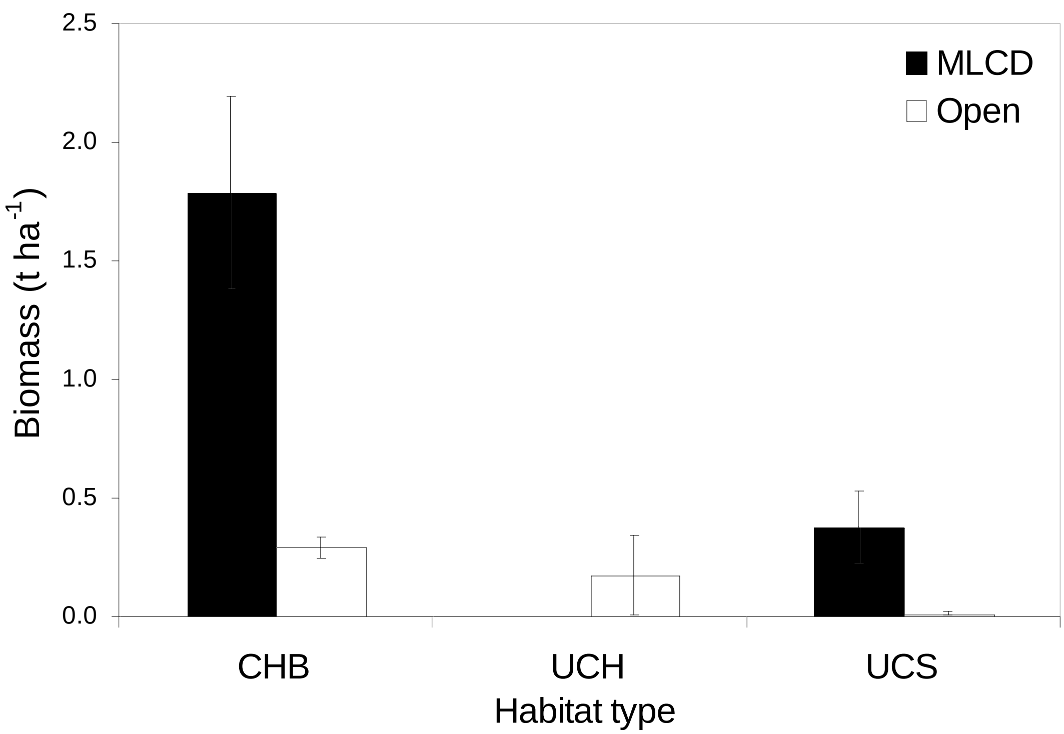

Figure 58. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the south Maui and Molokini Shoal study area. Error bars are standard error of the mean.

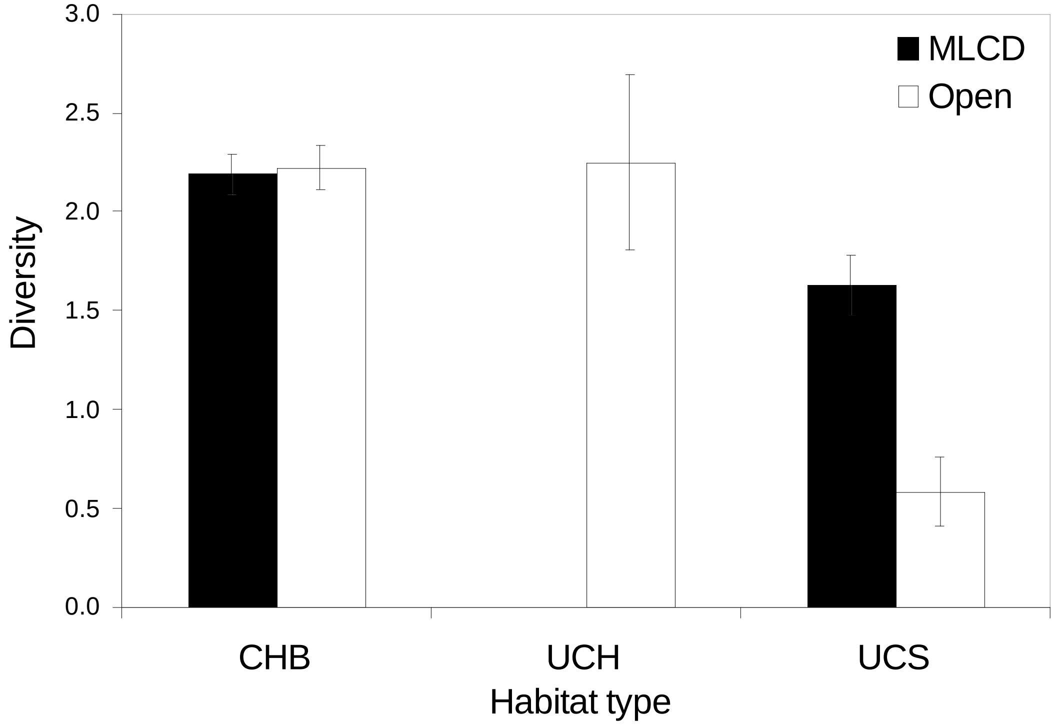

Figure 59. Mean diversity (H') per transect (125 m^2) by habitat type and management regime for the south Maui and Molokini Shoal study area. Error bars are standard error of the mean.

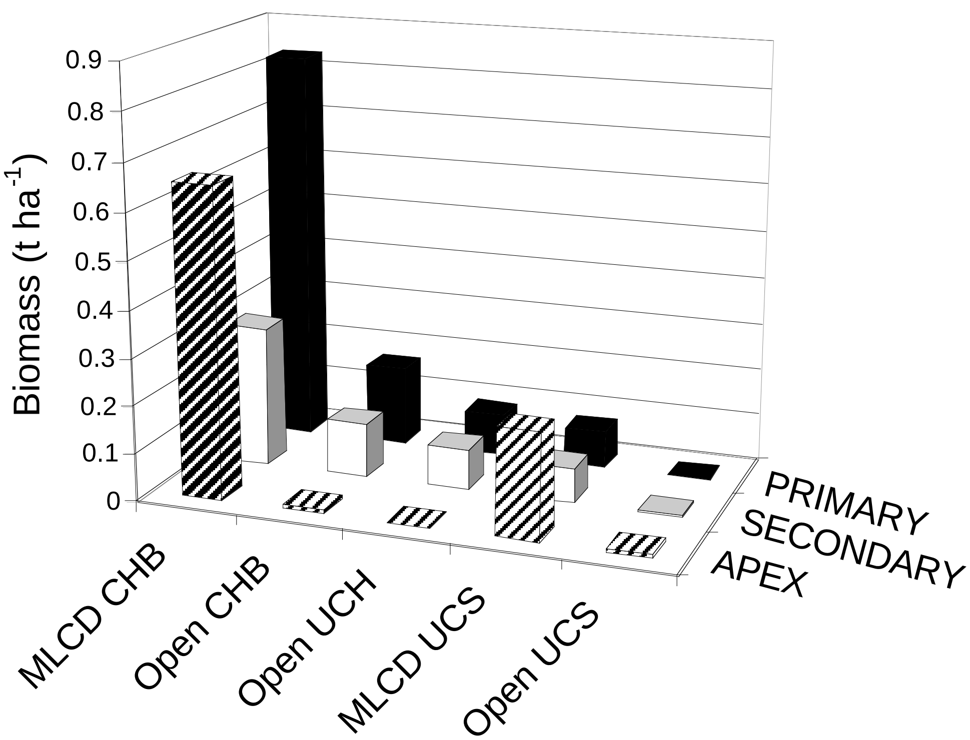

Figure 60. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the south Maui and Molokini Shoal study area.

Table 37. Top ten species in the Molokini Shoal MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.72	0.166	55.26	9.53	13.49	745.57
Melichthys niger	Black Durgon	*humuhumuelele*	0.39	0.164	39.47	5.13	13.34	526.63
Triaenodon obesus	Whitetip Reef Shark	*mano lalakea*	0.01	0.286	15.79	0.17	23.26	367.33
Caranx melampygus	Blue Trevally	*omilu*	0.04	0.098	34.21	0.58	7.95	271.91
Melichthys vidua	Pinktail Durgon	*humuhumuhiukole*	0.07	0.033	50.00	0.97	2.68	133.98
Xanthichthys auromarginatus	Gilded Triggerfish		0.23	0.033	36.84	3.01	2.67	98.36
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.09	0.030	39.47	1.23	2.43	96.04
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.09	0.024	34.21	1.23	1.98	67.65
Scarus psittacus	Palenose Parrotfish	*uhu*	0.54	0.015	42.11	7.13	1.20	50.62
Monotaxis grandoculis	Bigeye Emperor	*mu*	0.01	0.030	15.79	0.17	2.47	38.98

Table 38. Top ten species in the south Maui open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.78	0.029	68.18	15.73	12.89	878.62
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.52	0.023	50.00	10.39	10.34	517.04
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.52	0.013	72.73	10.46	5.65	410.86
Scarus psittacus	Palenose Parrotfish	*uhu*	0.24	0.018	40.91	4.83	8.06	329.80
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.08	0.018	40.91	1.68	7.94	324.98
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.21	0.009	40.91	4.32	4.24	173.44
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.08	0.014	27.27	1.68	6.12	167.04
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.06	0.007	40.91	1.17	3.23	132.02
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.07	0.011	22.73	1.32	4.87	110.63
Melichthys vidua	Pinktail Durgon	*humuhumuhiukole*	0.02	0.008	22.73	0.37	3.74	84.96

Manele-Hulopoe MLCD and south Lanai

The south Lanai study area extended from Palaoa Point to Manele Bay (ca. 10.2km) and included the Manele-Hulopoe MLCD.

Sample allocation

A total of 73 samples were collected between October 28 and March 5, 2003 (Fig. 61; Table 39). The two levels of sampling stratification included major habitat types (CHB, UCH and UCS) and fisheries management regime (open access and MLCD). No macroalgae polygons (minimum mapping unit = one acre) occurred within the study area.

Table 39. Sample allocation for south Lanai study area.

Habitat	Open	MLCD	Total
Colonized hardbottom	19	12	31
Uncolonized hardbottom	10	11	21
Sand	11	10	21
Total	40	33	73

Large-scale benthic cover

Benthic coverage for Manele-Hulopoe MLCD derived from the NOAA benthic habitat maps consisted primarily of sand (39%), followed by colonized volcanic rock and boulder (31%) and uncolonized volcanic rock and boulder (26%) (Table 40).

Table 40. Benthic cover for the Manele-Hulopoe MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Artificial	Manmade feature	929	0.08
Colonized hardbottom	Aggregated coral	19279	1.73
	Colonized volcanic rock/boulder	344888	30.87
Mud		6700	0.60
Sand		437656	39.17
Uncolonized Hardbottom	Uncolonized pavement	14991	1.34
	Uncolonized volcanic rock/boulder	292914	26.21
Grand total		1117358	100.00

Small-scale benthic cover of substrate types within the management regimes.
The most abundant substrate type was turf algae (MLCD - 42%, Open - 48%), followed by Sand (MLCD - 33%, Open - 27%) (Table 41; Fig. 62). Total coral cover was 20% in the MLCD and 13% in the open areas. *Porites lobata* (7%), *Montipora patula* (6%), *P. compressa* (3%), and *Pocillopora meandrina* (2%) were the primary coral species in the MLCD compared to *Pocillopora meandrina* (5%), *Porites lobata* (5%), and *Montipora patula* (2%) in the open access areas. Cover of coralline algae was similar between the MLCD (4%) and open areas (5%). Macroalgae was scarce, with less than 1% cover in both the MLCD and the open access area. The remaining macorinvertebrates were less than 1% of the benthic cover

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types (Fig. 62). This result indicated that comparing fish assemblages across the management strata was appropriate at the major subtrate types.

Fish assemblage characteristics among habitat types and between management regimes
Values for species richness, biomass, and diversity were all moderately high along the entire coastline (Fig. 63, 64, and 65). Fish assemblage characteristics were not significantly different between the MLCD and the open area over all habitat types (Fig. 66, 67, and 68; Table 42A, 42B, and 42C). Assemblage characteristics were comparable between the uncolonized and colonized habitat types, although biomass was significantly greater ($p<0.05$) in the uncolonized MLCD habitat compared with the uncolonized open area (Table 42B).

Fish trophic structure between management regimes and among habitats
Herbivores were the dominant trophic guild by weight over all habitat types, accounting for over 68% of the total fish biomass (Fig. 69). These were followed by secondary consumers (24%) and apex predators (8%). Apex predator biomass was twice as high in the MLCD compared with the open area. In the uncolonized hardbottom habitat, herbivores biomass was nearly 75% greater in the MLCD compared with the open access areas.

Species composition by management regime
Nine of the top ten species in the MLCD were parrotfishes or surgeonfishes, the one exception being the introduced peacock grouper (*roi*, *Cephalopholis argus*) (Table 43). The open area had a somewhat similar species composition with the exception of the small saddle wrasse (*hinalea lauwili*) and blackfin chromis (*Chromis vanderbilti*), which were frequently encountered (Table 44). Whitebar surgeonfish (*Maikoiko*) were the most important species by weight in both the MLCD (10%) and the open area (9%), followed by orangespine unicornfish (*umaumalei*, 9% in the MLCD and 7% in the open area). The prized bluefin trevally (*omilu*, *Caranx melampygus*) accounted for 5% of the fish biomass within the MLCD.

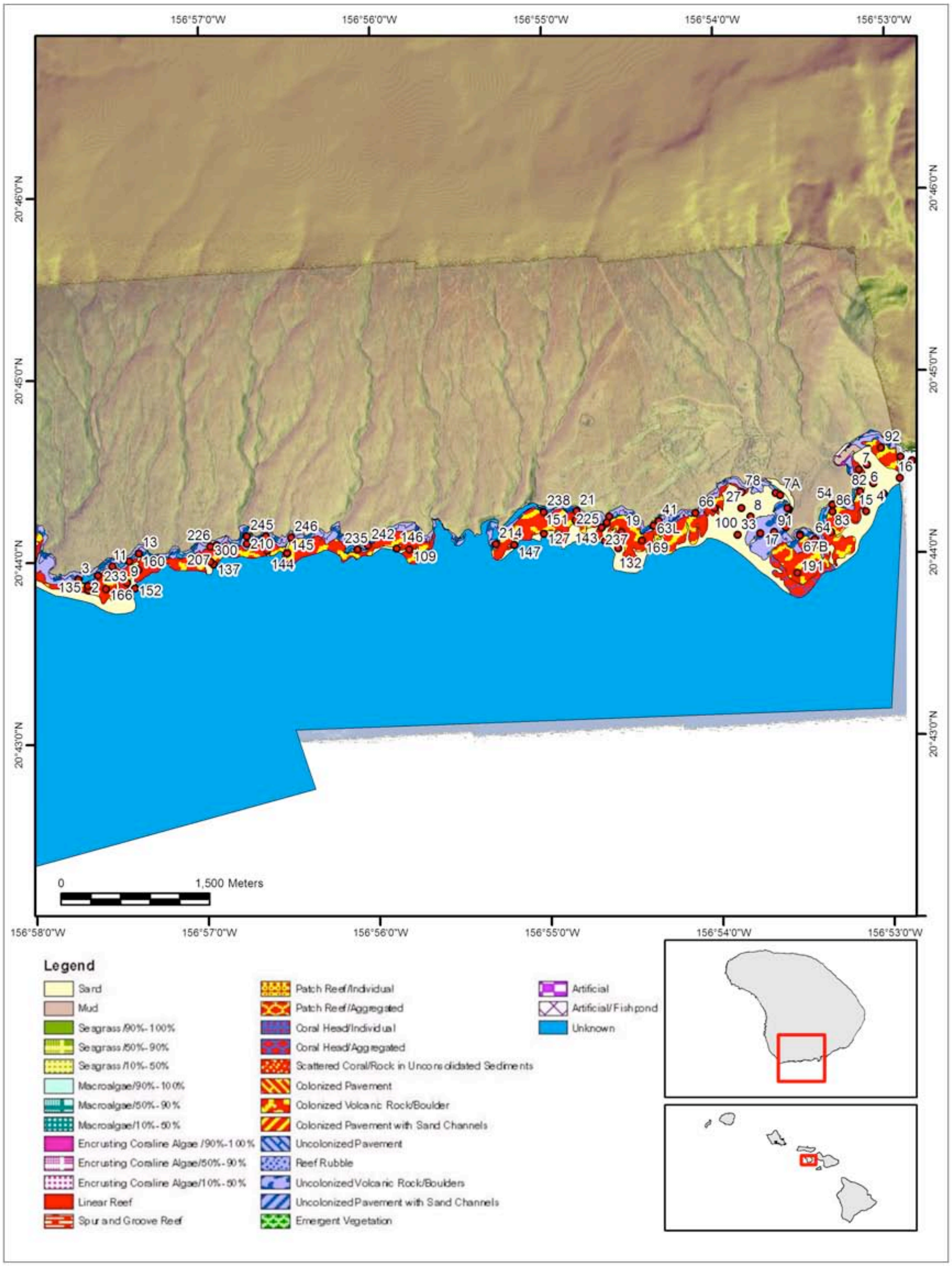

Figure 61. Sampling locations and benthic habitats for the Manele-Hulopoe MLCD and adjacent areas

Table 41. Top 10 benthic taxa/substrate types by percent cover within the Manele Bay-Hulopoe Marine Life Conservation District (MLCD) and the open access area outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		41.7	Turf algae		47.6
Sand		33.1	Sand		27.2
Coral	*Porites lobata*	7.0	Silt		6.1
Coral	*Montipora patula*	6.0	Coral	*Pocillopora meandrina*	5.4
Coralline algae		4.5	Coral	*Porites lobata*	5.2
Coral	*Porites compressa*	3.3	Coralline algae		5.1
Coral	*Pocillopora meandrina*	1.9	Coral	*Montipora patula*	1.8
Coral	*Montipora capitata*	0.9	Coral	*Montipora capitata*	0.5
Coral	*Pavona duerdeni*	0.4	Macroalgae	*Halimeda sp.*	0.4
Coral	*Pavona varians*	0.3	Macroalgae		0.2

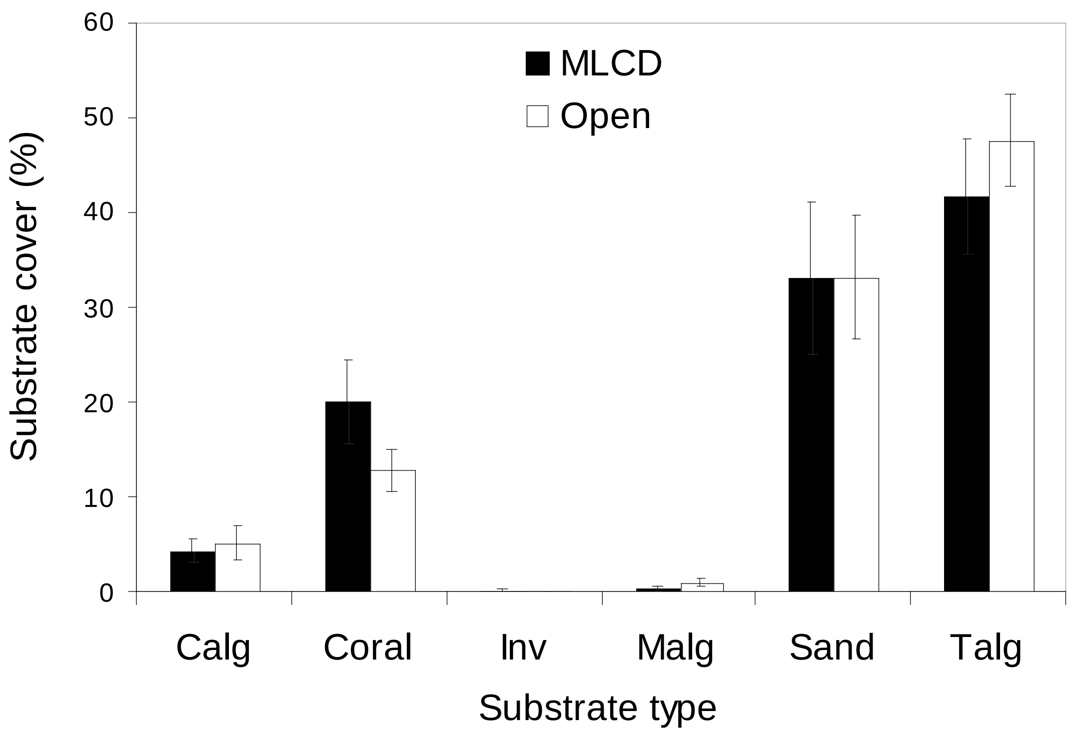

Figure 62. Mean percent cover of substrate types within the Manele Bay-Hulopoe Bay Marine Life Conservation District (MLCD) and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

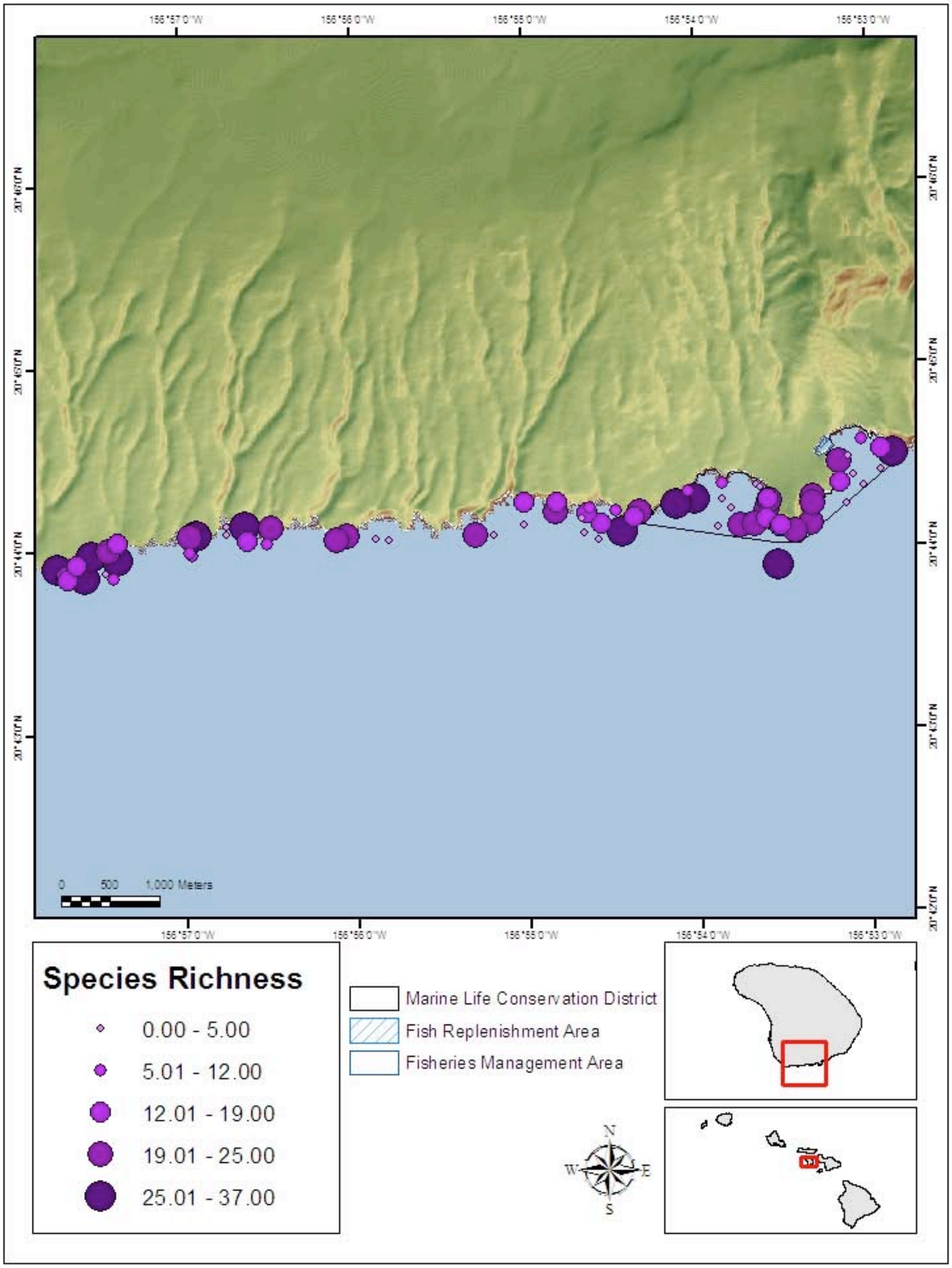

Figure 63. Species richness by individual transects (N=73) for the south Lanai study area, including Manele-Hulopoe MLCD. Classification based on quantiles.

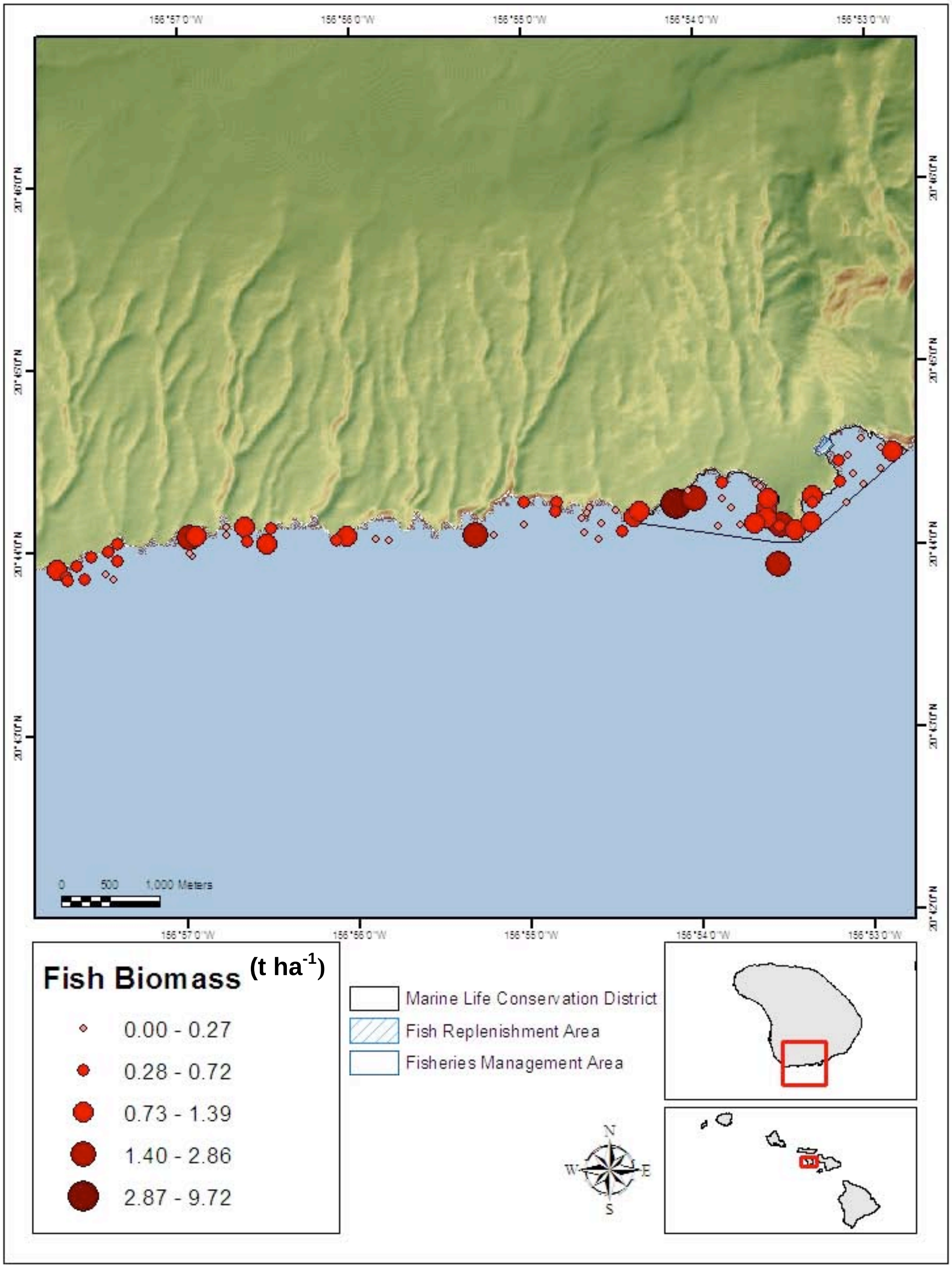

Figure 64. Fish biomass (t ha^{-1}) by individual transects (N=73) for the south Lanai study area, including Manele-Hulopoe MLCD. Classification based on quantiles.

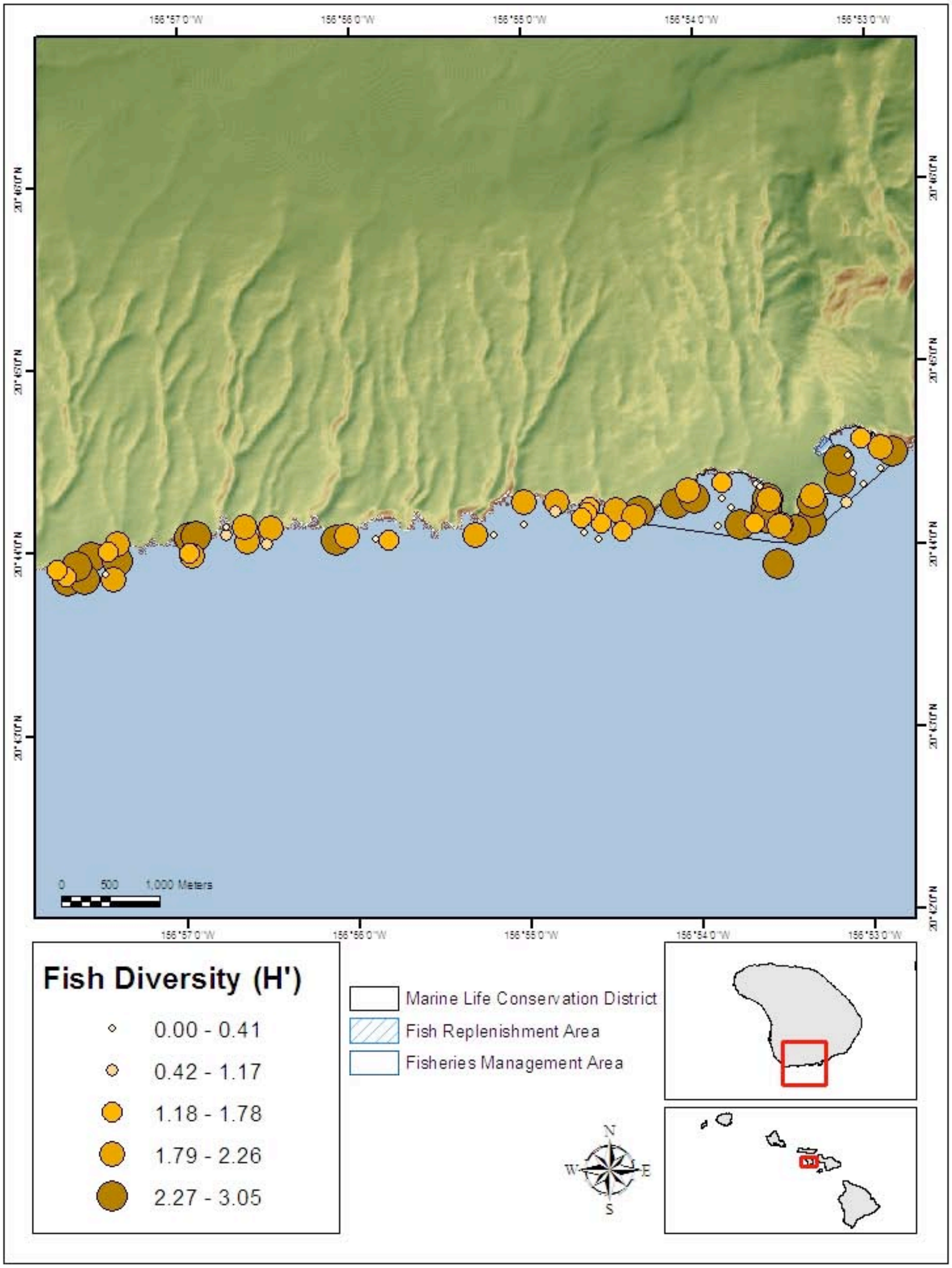

Figure 65. Fish diversity (H') by individual transects (N=73) for the south Lanai study area, including Manele-Hulopoe MLCD. Classification based on quantiles.

Table 42A. Comparison of fish species richness among management regimes and habitat types for the south Lanai study area. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 73). Management regimes: MLCD ([M]) and Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB), <10% live coral hard bottom (UCH), and unconsolidated sediments (UCS). Unplanned multiple comparisons among management strata and habitat$_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different (α = 0.05)

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	1122	40.6	<0.001	
Management	1	4	0.1	0.70	MLCD = Open
Habitat$_{[management]}$	4	1399	50.6	<0.001	
Error	67	27			
Habitat$_{[management]}$ -					CHB$_{[O]}$ UCH$_{[M]}$ CHB$_{[M]}$ UCH$_{[O]}$ UCS$_{[O]}$ UCS$_{[M]}$

Table 42B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the south Lanai study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	0.83	12.0	<0.0001	
Management	1	0.22	3.5	0.07	MLCD = Open
Habitat$_{[management]}$	4	1.00	15.6	<0.0001	
Error	67	0.06			
Habitat$_{[management]}$ -					UCH$_{[M]}$ CHB$_{[O]}$ CHB$_{[M]}$ UCH$_{[O]}$ UCS$_{[O]}$ UCS$_{[M]}$

Table 42C. Comparison of fish species diversity (H') among management regimes and habitat types for the south Lanai study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	10.4	44.4	<0.001	
Management	1	0.1	0.3	0.58	MLCD = Open
Habitat$_{[management]}$	4	12.9	55.4	<0.001	
Error	67	0.2			
Habitat$_{[management]}$ -					UCH$_{[M]}$ CHB$_{[M]}$ UCH$_{[O]}$ CHB$_{[O]}$ UCS$_{[O]}$ UCS$_{[M]}$

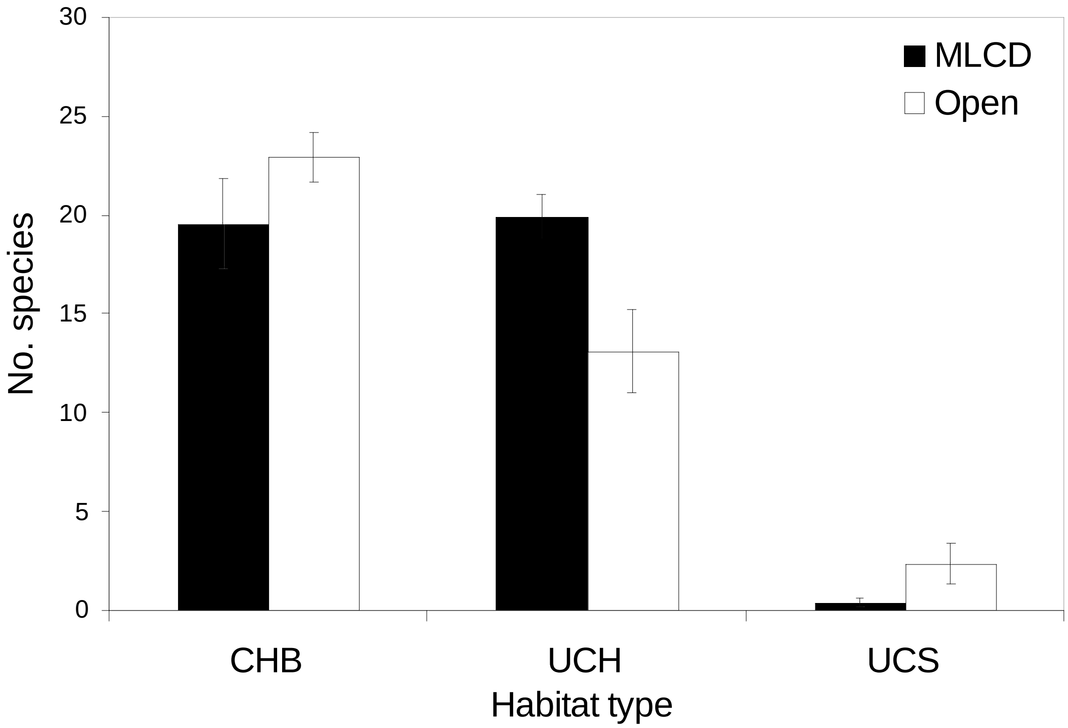

Figure 66. Mean number of species per transect (125 m^2) by habitat type and management regime for the south Lanai study area. Error bars are standard error of the mean.

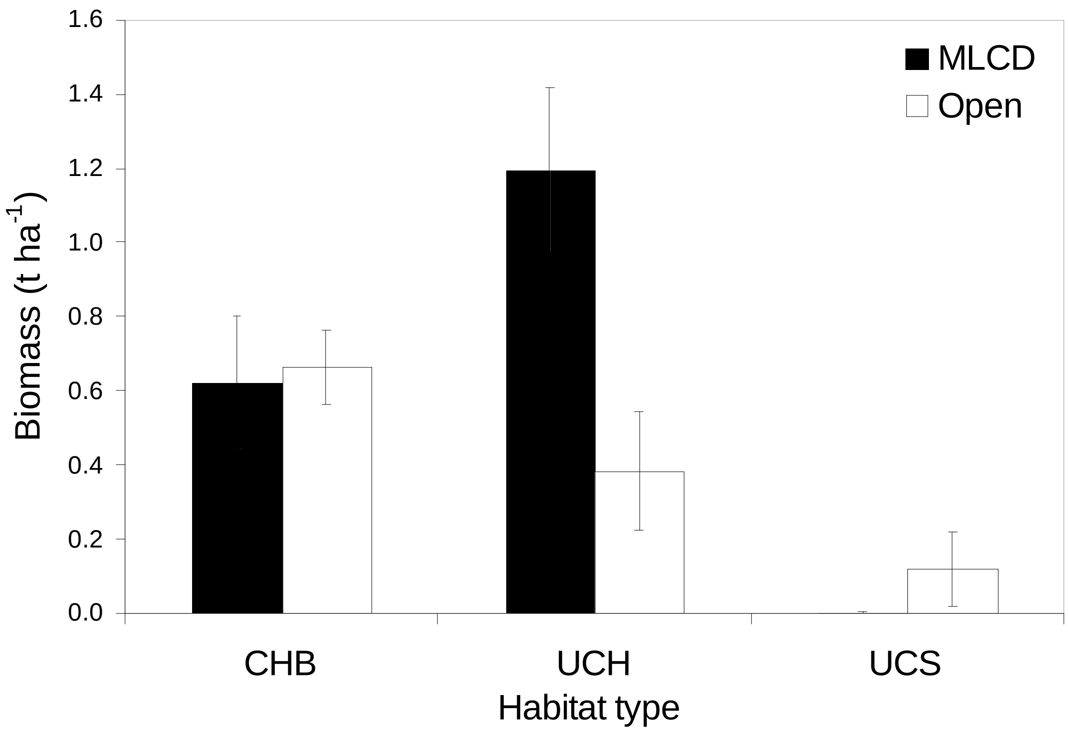

Figure 67. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the south Lanai study area. Error bars are standard error of the mean.

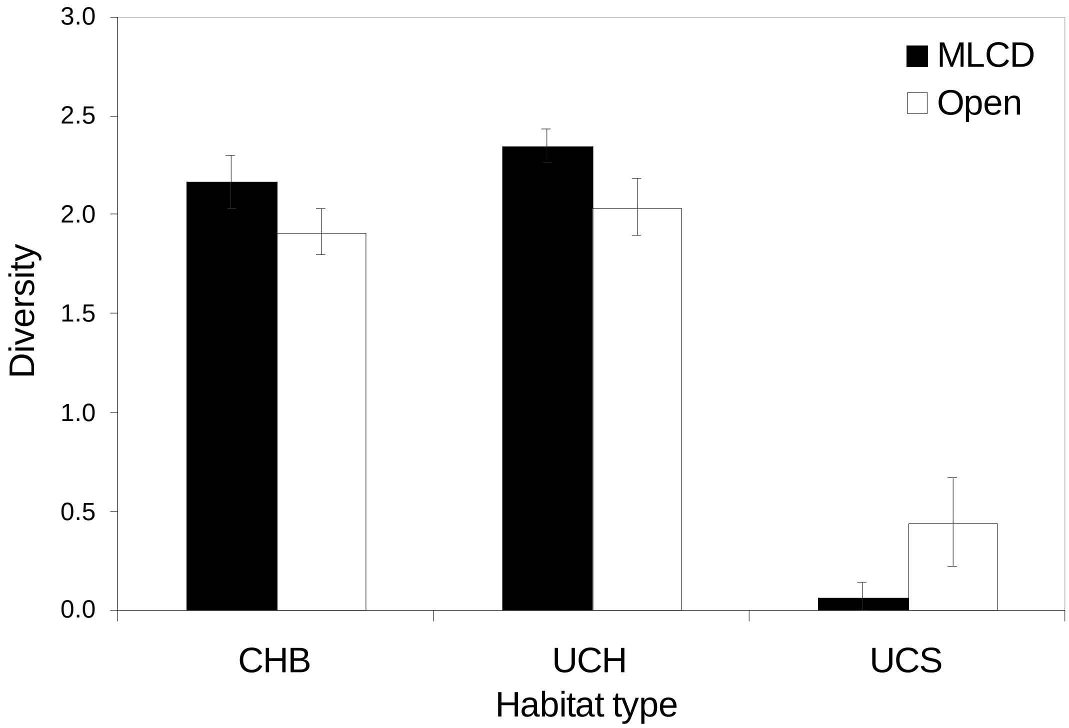

Figure 68. Mean diversity (H') per transect (125 m^2) by habitat type and management regime for the south Lanai study area. Error bars are standard error of the mean

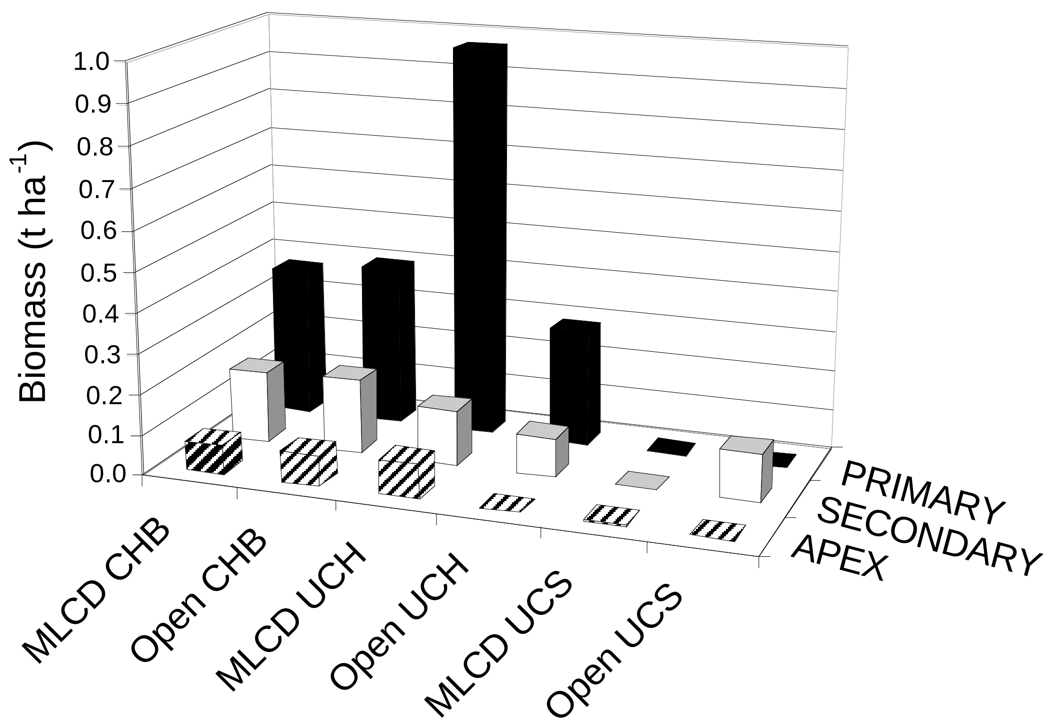

Figure 69. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the south Lanai study area.

Table 43. Top ten species in the Manele-Hulopoe MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.17	0.054	51.52	2.74	8.60	443.08
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.39	0.061	42.42	6.36	9.81	416.24
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.35	0.034	54.55	5.81	5.38	293.35
Acanthurus triostegus	Convict Tang	*manini*	0.51	0.051	27.27	8.39	8.23	224.49
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.37	0.017	63.64	6.13	2.73	173.60
Acanthurus achilles	Achilles Tang	*pakuikui*	0.21	0.035	30.30	3.50	5.56	168.47
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.41	0.023	39.39	6.68	3.72	146.61
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.11	0.025	33.33	1.75	4.05	135.13
Chlorurus perspicillatus	Spectacled Parrotfish	*uhu uliuli*	0.03	0.037	21.21	0.48	5.94	125.98
Cephalopholis argus	Blue-spotted Grouper		0.04	0.025	30.30	0.68	3.97	120.18

Table 44. Top ten species in the south Lanai open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.12	0.032	55.00	1.36	7.22	397.19
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.55	0.018	67.50	6.45	4.06	274.19
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.24	0.040	25.00	2.85	9.06	226.38
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.24	0.022	42.50	2.76	5.06	214.90
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.31	0.027	30.00	3.67	6.15	184.48
Scarus psittacus	Palenose Parrotfish	*uhu*	0.22	0.021	37.50	2.62	4.78	179.26
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.47	0.010	72.50	5.52	2.34	169.80
Acanthurus achilles	Achilles Tang	*pakuikui*	0.18	0.027	27.50	2.15	6.06	166.73
Chromis vanderbilti	Blackfin Chromis		4.05	0.012	52.50	47.28	2.64	138.86
Melichthys niger	Black Durgon	*humuhumuelele*	0.10	0.019	30.00	1.12	4.33	129.84

Old Kona Airport MLCD and Kailua Kona area

The north Kona study area extended from Noio Point to Keikiwaha Point (ca 20.4km) and included the Old Kona Airport MLCD, Papawai Bay FMA, and Kailua-Keauhou FRA.

Sample allocation

A total of 73 samples were collected between December 2 and March 18, 2003 (Table 45; Fig. 70A and 70B). The two levels of sampling stratification included major habitat types (CHB, UCH and UCS) and fisheries management regimes (open access, MLCD, and FMA). No macroalgae polygons (minimum mapping unit = one acre) occurred within the study area. The Papawai Bay FMA and Kailua_Keauhou FRA were both included in the FMA stratum.

Table 45. Sample allocation for Kailua Kona study area.

Habitat	FMA	MLCD	Open	Total
Colonized hardbottom	12	10	10	32
Uncolonized hardbottom	10	11	10	31
Unconsolidated sediment	10			10
Total	32	21	20	73

Large-scale benthic cover

Benthic coverage for Old Kona Airport MLCD derived from the NOAA benthic habitat maps consisted primarily of colonized volcanic rock/boulder (42%) and sand (42%), followed by uncolonized volcanic rock and boulder (16%) (Table 46).

Table 46. Benthic cover for the Old Kona Airport MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized hardbottom	Colonized volcanic rock/boulder	443727	41.92
Sand		440935	41.65
Uncolonized hardbottom	Uncolonized volcanic rock/boulder	173944	16.43
Grand total		1058606	100.00

Small-scale benthic cover of substrate types within the management regimes.

The most abundant substrate type in all 3 strata was turf algae, which averaged 65% cover in the MLCD, 72% in the open access area, and 46 % in the FMA (Table 47; Fig. 71). Total coral cover averaged 24% in the MLCD, 17% in the open access area, and 11% in the FMA. *Porites lobata, P. compressa,* and *Pocillopora meandrina* were the primary coral species found in the 3 management strata. Sand was prevalent in the FMA (32%), but occupied less than 1% of the substrate in the MLCD and the open access areas. Coralline algae cover was similar among the management strata with 5% in the MLCD and 4% in both the open access area and FMA. Macorinvertebrates were quite abundant at this site, with *Anthelia edmondsonii* predominant among the management regimes. *Echinometra mathaei* was also prevalent and corresponded to the low (<1%) macroalgae cover.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types except for sand, which was nearly 50 times more abundant in the FMA than in the other two management strata (Table 47; Fig. 71). Consequently, the FMA habitats were considered distinct from the MLCD and the open access area and factored into the comparisons of the fish assemblages.

Fish assemblage characteristics among habitat types and management regimes

Higher values for species richness, biomass, and to a lesser extent, diversity were observed in the northern portion of the study areas (Fig. 72, 73, and 74). Species richness and biomass were significantly higher in the MLCD compared to the FMAs and open area (Fig. 75 and 76; Table 48A and 48B), while diversity (Table 48C; Fig. 77) showed no significant difference among management regimes ($p>0.05$). Colonized hardbottom in the MLCD had the highest species richness, while the uncolonized hardbottom within the MLCD had the highest biomass and diversity. The uncolonized FMA habitat had the lowest values for both species richness and biomass among the habitat types common to all three management regimes. Diversity did not vary significantly among management regimes ($p>0.05$) or habitat types ($p>0.05$).

Fish trophic structure between management regimes and among habitats

Herbivores accounted for over 66% of the total fish biomass among all habitat types and management regimes, followed by secondary consumers (31%), and apex predators (3%) (Fig. 78). Apex predators were four times more abundant by weight in the MLCD compared to the FMAs and more than two times more abundant than in the open area. This trophic group was comprised primarily of the introduced roi. Herbivores were most abundant in the uncolonized hardbottom habitat while secondary consumers were more abundant in the colonized hardbottom habitats.

Species composition by management regime

A number of surgeonfishes dominated the fish assemblage in the MLCD, including: yellow tang (*lauipala*, *Zebrasoma flavescens*), orangeband surgeonfish (*naenae*), goldring surgeonfish (*kole*), whitebar surgeonfish (*maikoiko*), brown surgeonfish (*maiii*) and orangespine unicornfish (*umaumalei*) (Table 49). A similar mix of species dominated both the FMAs (Table 50) and open areas (Table 51), with lauipala, maiii, and kole having the highest IRD, respectively, in both management strata. The palenose parrotfish (*uhu*, *Scarus psittacus*) was nearly twice as abundant, by weight, in the MLCD compared with the open area and five times more abundant than in the FMAs.

Table 47. Top 10 benthic taxa/substrate types by percent cover within the Old Kona Airport Marine Life Conservation District (MLCD), the open access area outside the MLCD, and inside of the adjacent Fisheries Management Area.

Marine Life Conservation District			Open Access			Fisheries Management Area		
Substrate Type	Taxon	%	Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		64.8	Turf algae		72.1	Turf algae		45.9
Coral	*Porites lobata*	19.0	Coral	*Porites lobata*	10.1	Sand		32.1
Coralline algae		5.0	Coral	*Pocillopora meandrina*	6.7	Coral	*Porites lobata*	10.1
Macroinvertebrate	*Anthelia edmondsonii*	4.8	Coralline algae		4.2	Coralline algae		3.6
Coral	*Porites compressa*	4.1	Coral	*Porites compressa*	2.0	Macroinvertebrate	*Anthelia edmondsonii*	3.3
Coral	*Montipora capitata*	0.5	Macroinvertebrate	*Anthelia edmondsonii*	1.3	Coral	*Pocillopora meandrina*	1.7
Sand		0.5	Coral	*Porites evermanni*	0.9	Coral	*Porites compressa*	1.6
Coral	*Porites evermanni*	0.4	Coral	*Montipora patula*	0.7	Macroinvertebrate	*Echinometra mathaei*	0.4
Macroinvertebrate	*Echinometra mathaei*	0.3	Sand		0.7	Macroalgae		0.4
Coral	*Pocillopora meandrina*	0.2	Coral	*Montipora capitata*	0.4	Coral	*Montipora capitata*	0.3

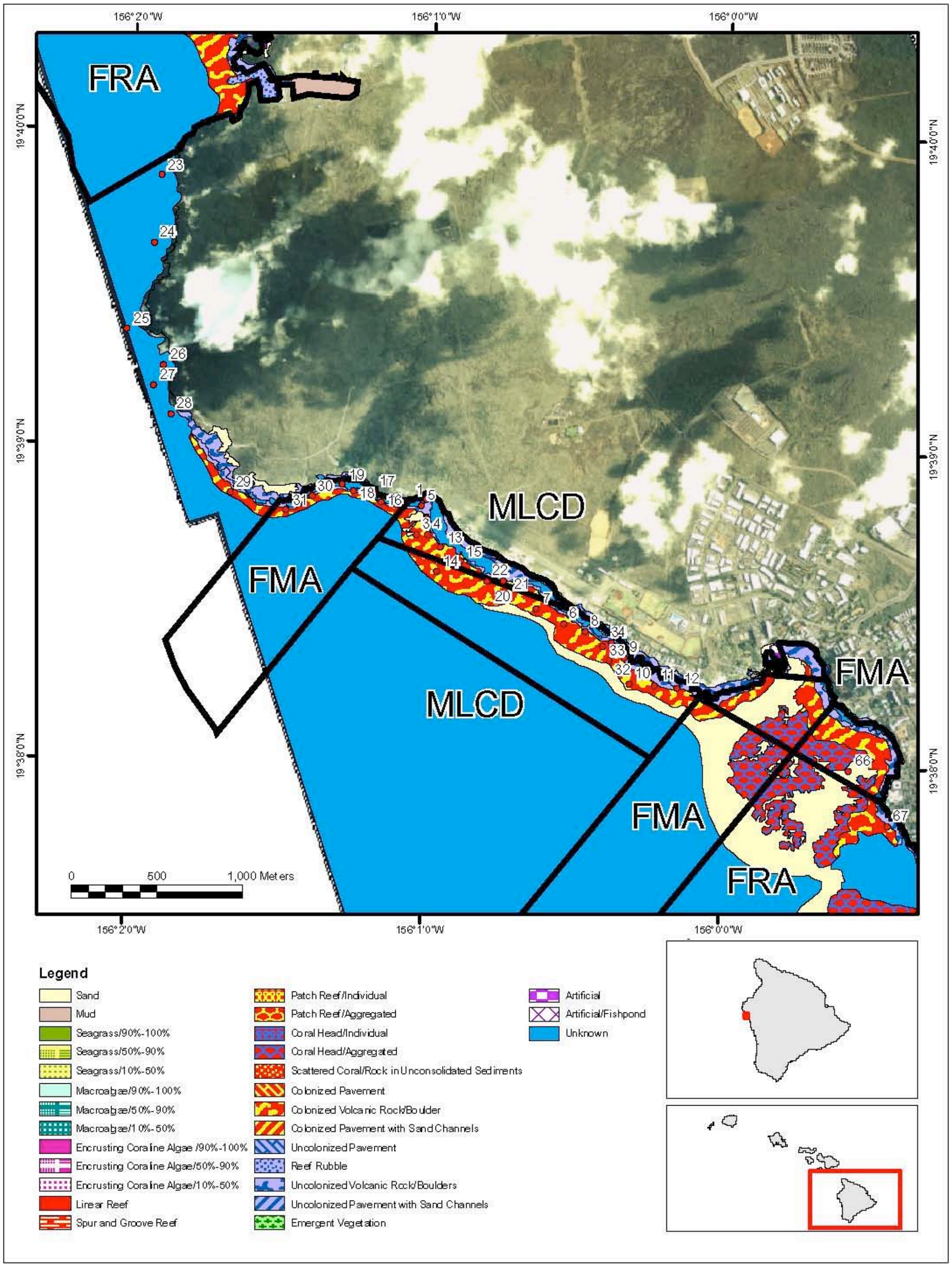

Figure 70A. Sampling locations and benthic habitats for the Old Kona Airport MLCD and adjacent areas. FMA = Fisheries Management Areas, FRA = Fish Replenishment Areas.

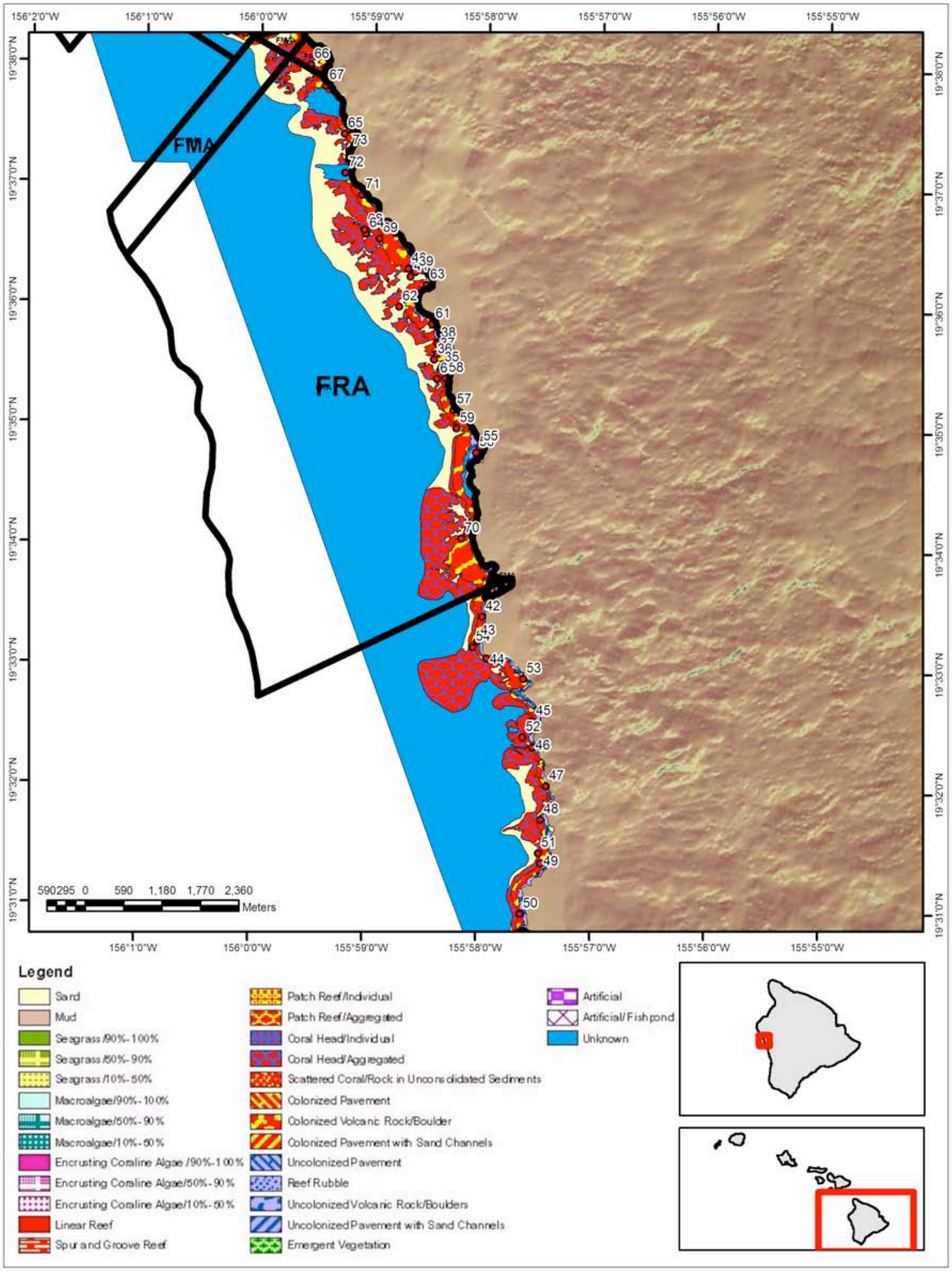

Figure 70B. Sampling locations and benthic habitats for the Kailua-Kona study area. FMA = Fisheries Management Area, FRA = Fish Replenishment Area.

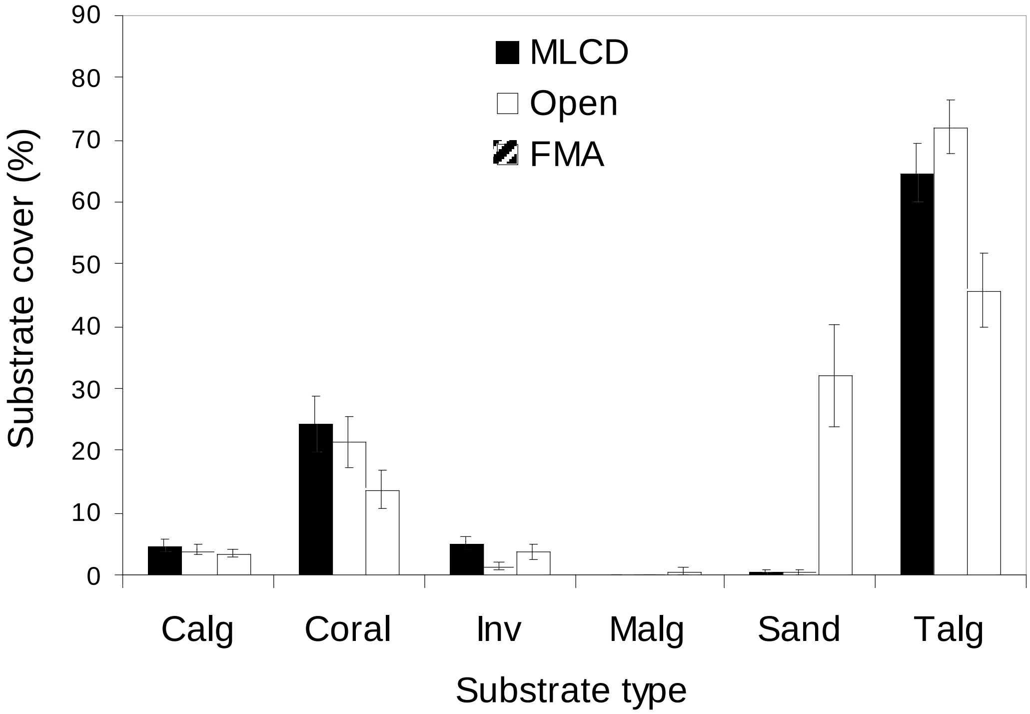

Figure 71. Mean percent cover of substrate types within the Old Kona Airport Marine Life Conservation District (MLCD), outside (Open) of the MLCD, and inside of the adjacent Fisheries Management Area (FMA). Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

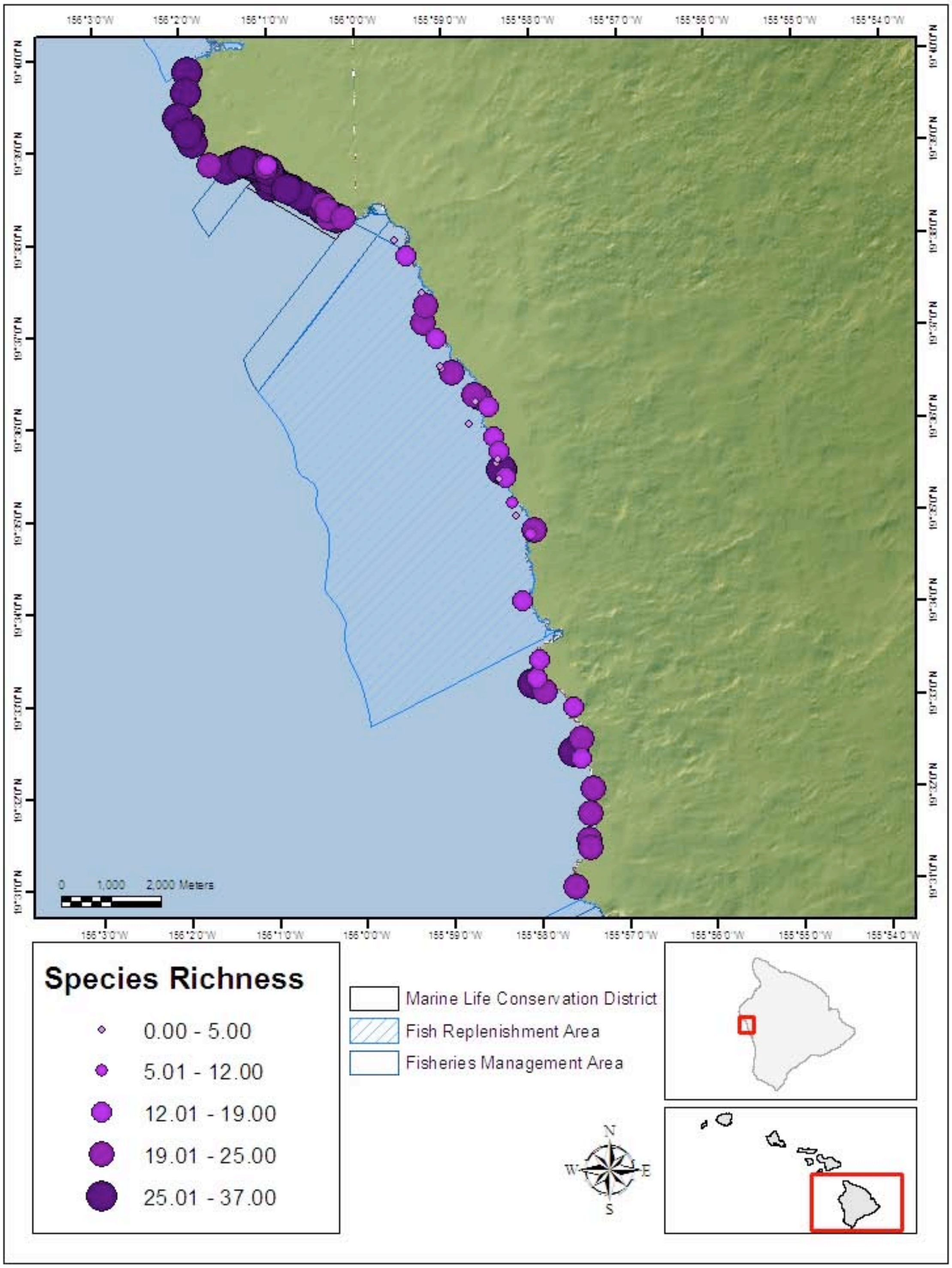

Figure 72. Species richness by individual transects (N=73) for the Kailua Kona study area, including Old Kona Airport MLCD. Classification based on quantiles.

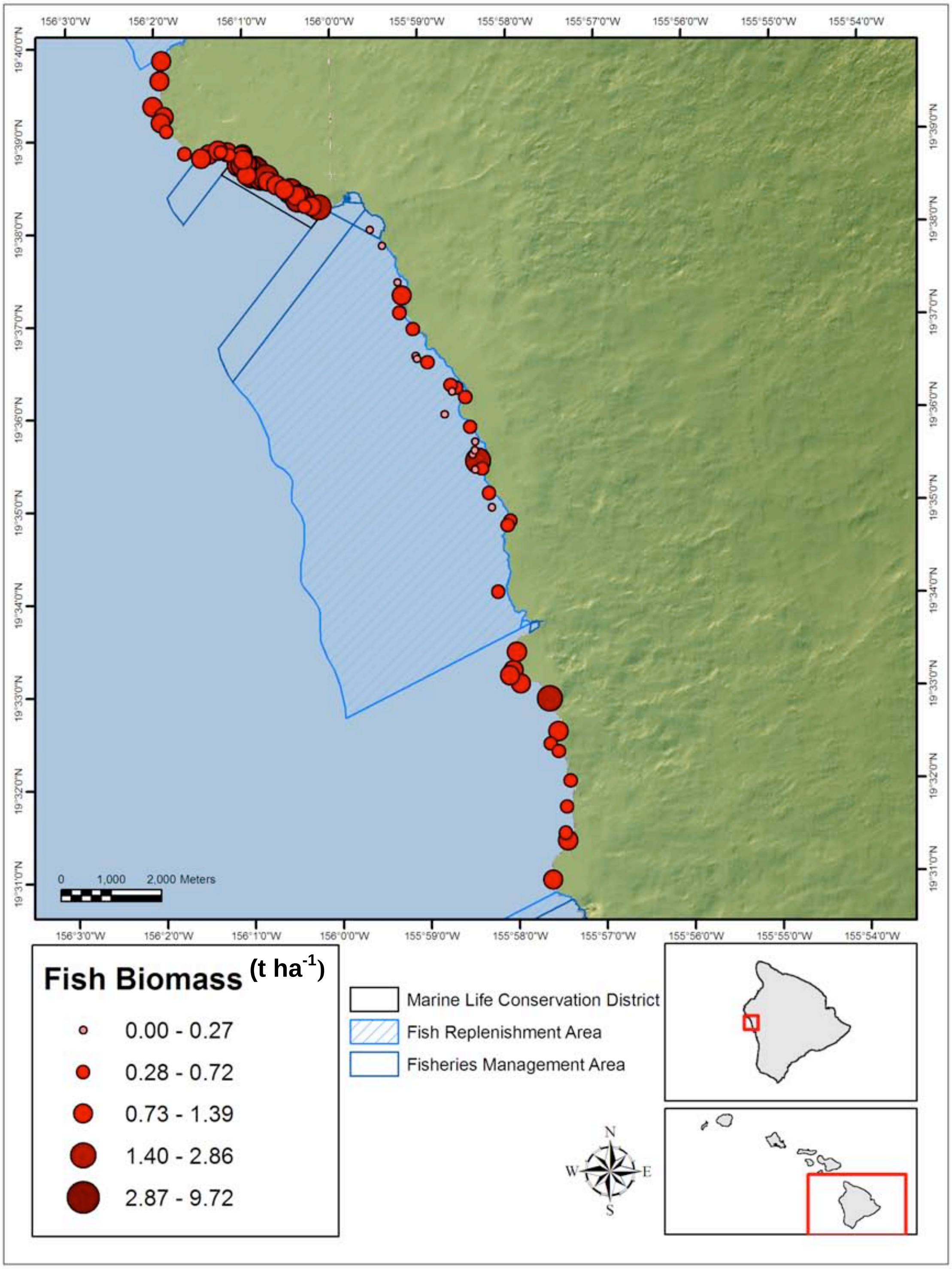

Figure 73. Fish biomass (t ha^{-1}) by individual transects (N=73) for the Kailua Kona study area, including Old Kona Airport MLCD. Classification based on quantiles.

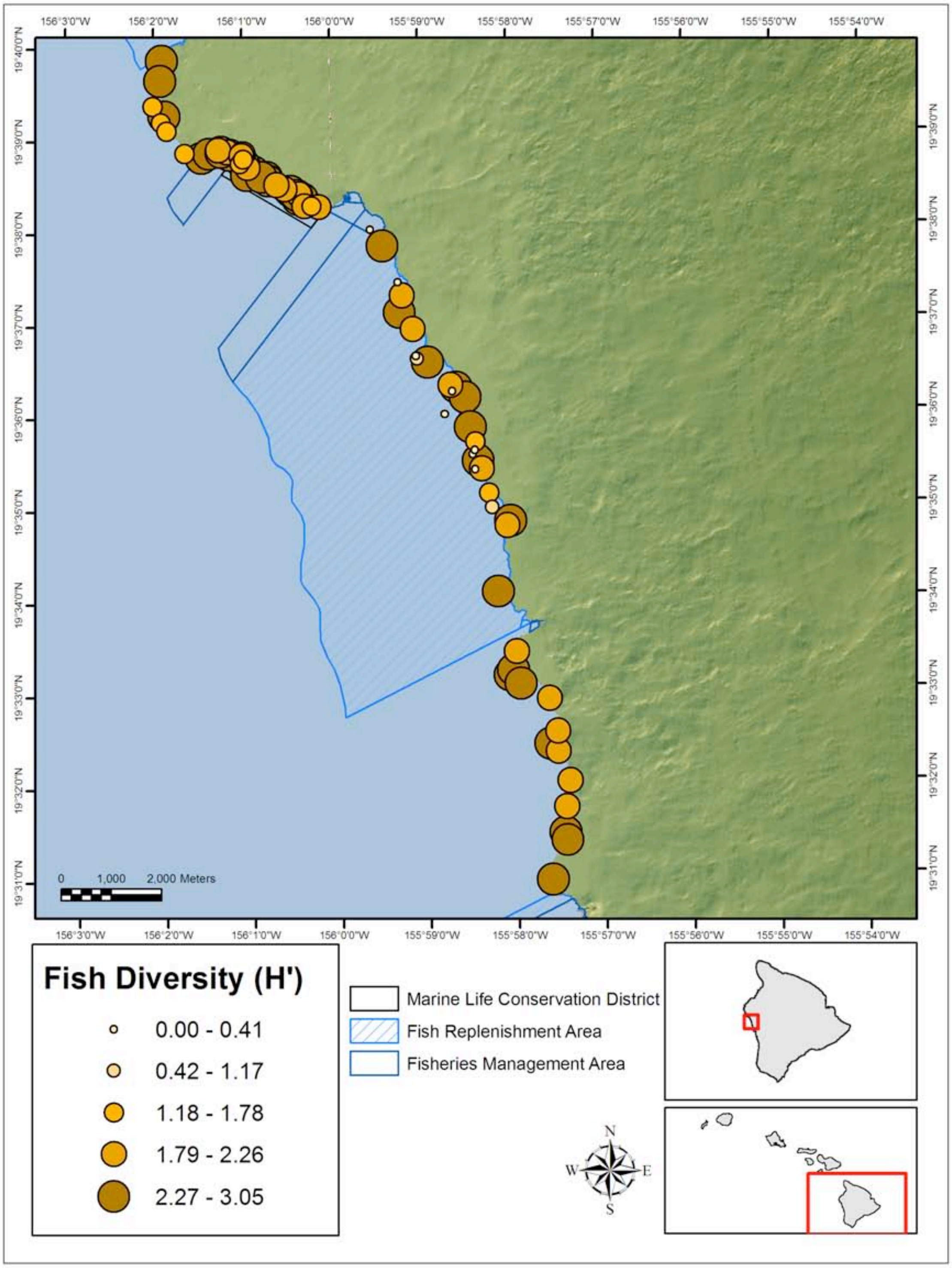

Figure 74. Fish diversity (H') by individual transects (N=73) for the Kailua Kona study area, including Old Kona Airport MLCD. Classification based on quantiles.

Table 48A. Comparison of fish species richness among management regimes and habitat types for the Kailua Kona study area. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 63). Management regimes: MLCD ([M]), FMA ([F]), and Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB) and <10% live coral hard bottom (UCH). Unplanned multiple comparisons among management strata and $habitat_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different ($\alpha = 0.05$)

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	209.9	9.7	<0.001	
Management	2	265.0	12.2	<0.001	MLCD > Open = FMA
$Habitat_{[management]}$	3	189.1	8.7	<0.001	
Error	57	28.3			
$Habitat_{[management]}$ -					$CHB_{[M]}$ $CHB_{[O]}$ $UCH_{[M]}$ $CHB_{[F]}$ $UCH_{[O]}$ $UCH_{[F]}$

Table 48B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the Kailua Kona study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	0.47	8.2	<0.001	
Management	2	0.85	14.9	<0.001	MLCD > Open = FMA
$Habitat_{[management]}$	3	0.21	3.6	0.02	
Error	57	0.05			
$Habitat_{[management]}$ -					$UCH_{[M]}$ $CHB_{[M]}$ $UCH_{[O]}$ $CHB_{[O]}$ $CHB_{[F]}$ $UCH_{[F]}$

Table 48C. Comparison of fish species diversity (H') among management regimes and habitat types for the Kailua Kona study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	0.15	1.1	0.39	
Management	2	0.07	0.5	0.63	FMA=MLCD=Open
$Habitat_{[management]}$	3	0.20	1.4	0.25	
Error	57	0.14			
$Habitat_{[management]}$ -					$UCH_{[M]}$ $CHB_{[F]}$ $UCH_{[F]}$ $UCH_{[O]}$ $CHB_{[M]}$ $CHB_{[O]}$

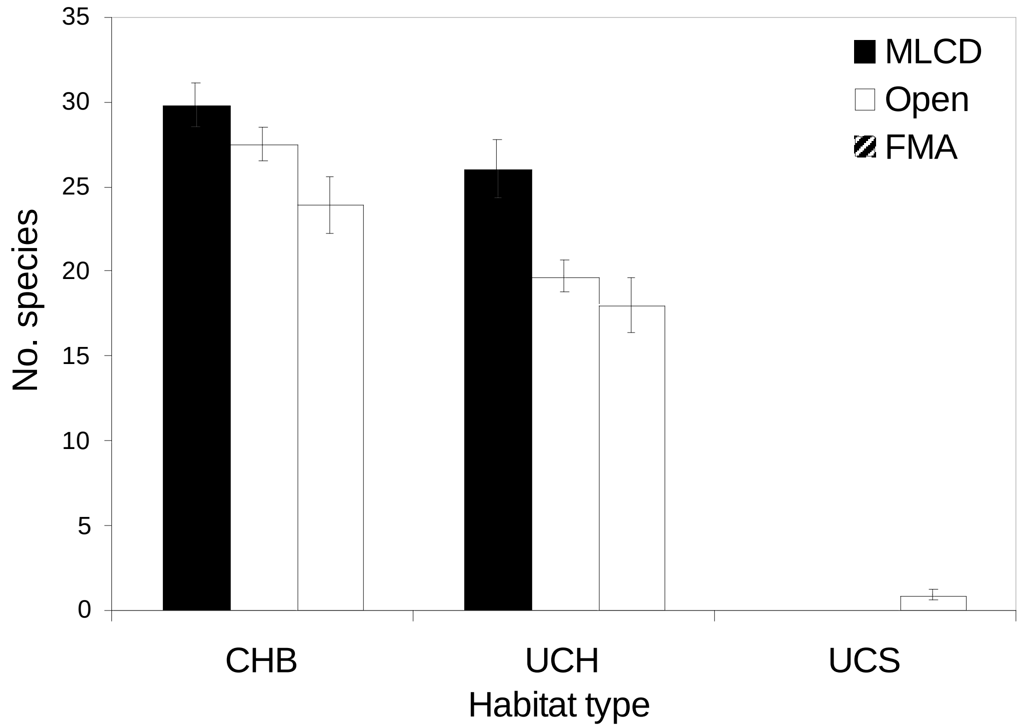

Figure 75. Mean number of species per transect (125 m^2) by habitat type and management regime for the Kailua Kona study area. Error bars are standard error of the mean.

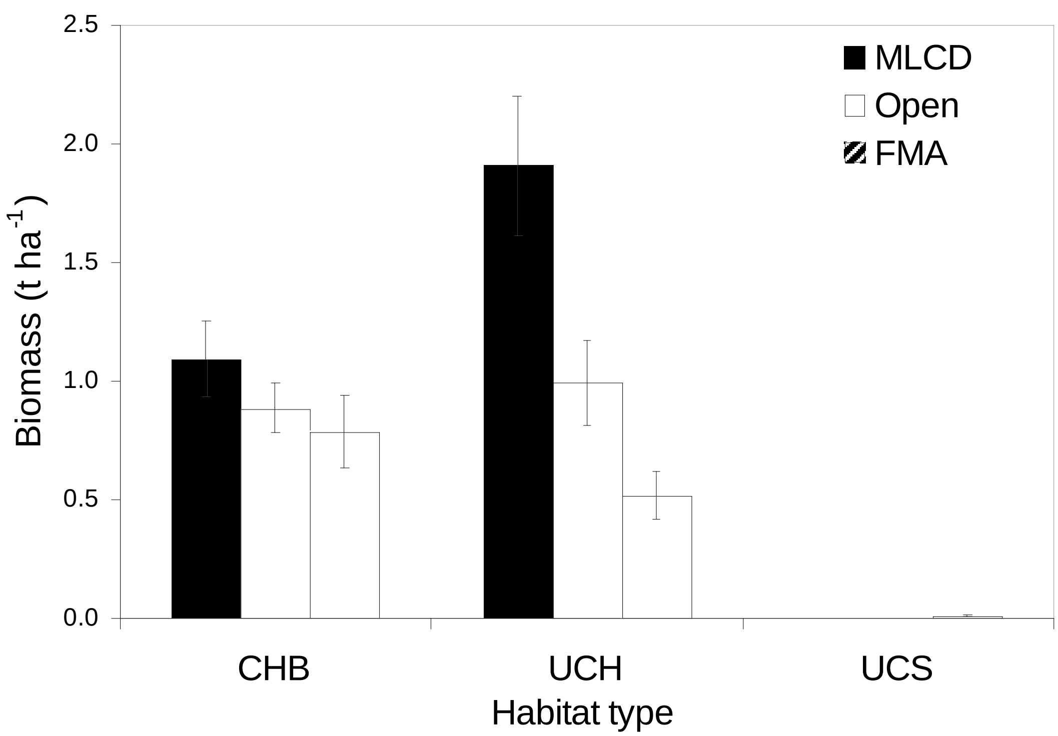

Figure 76. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the Kailua Kona study area. Error bars are standard error of the mean.

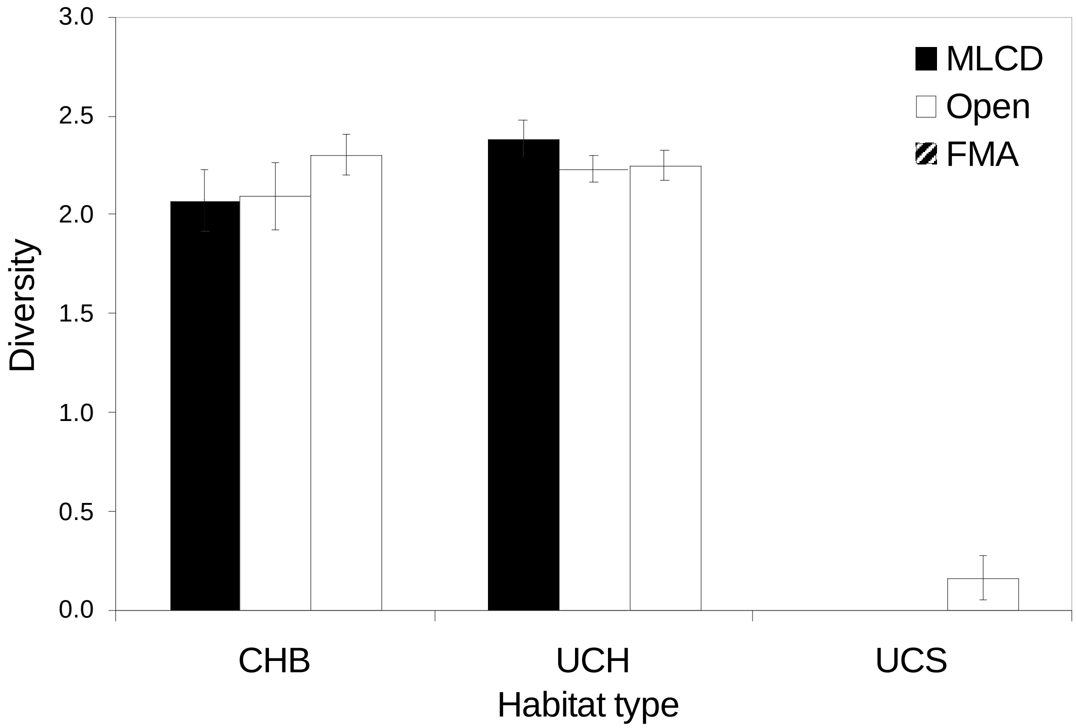

Figure 77. Mean diversity (H') per transect (125 m^2) by habitat type and management regime for the Kailua Kona study area. Error bars are standard error of the mean

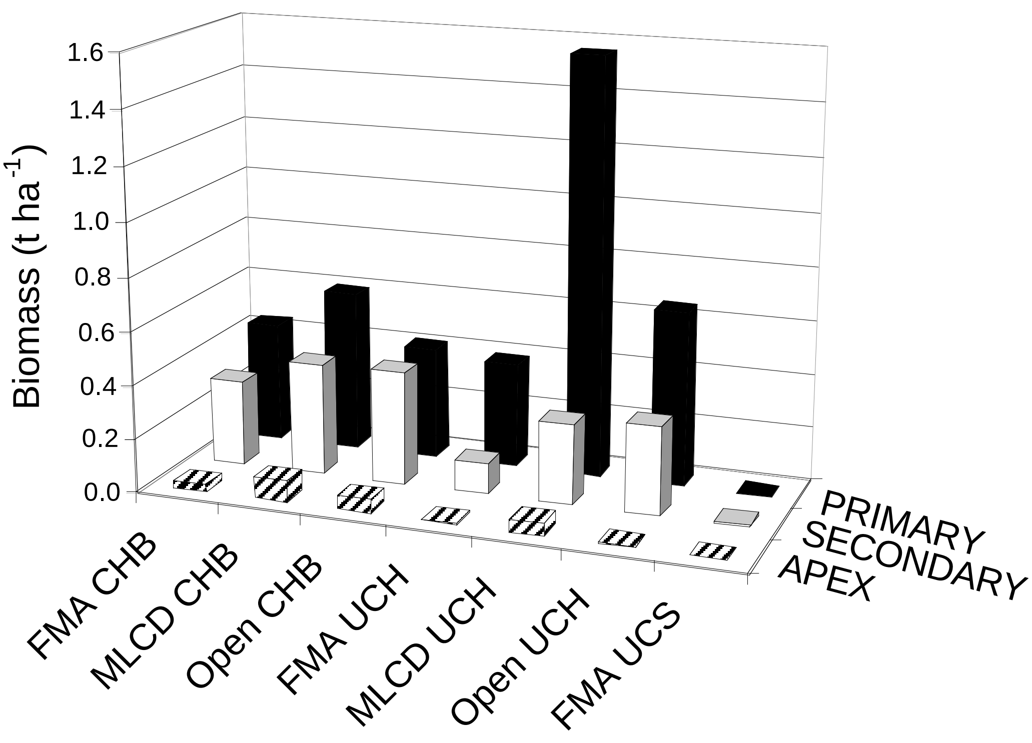

Figure 78. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the Kailua Kona study area.

Table 49. Top ten species in the Old Kona Airport MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Zebrasoma flavescens	Yellow Tang	*lauipala*	1.42	0.145	100.00	8.52	9.51	950.76
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.64	0.208	61.90	3.83	13.66	845.39
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	1.68	0.131	85.71	10.04	8.60	737.14
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.61	0.213	52.38	3.64	14.01	733.89
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	1.77	0.101	95.24	10.56	6.67	634.96
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.18	0.069	95.24	1.05	4.50	428.92
Melichthys niger	Black Durgon	*humuhumuelele*	0.25	0.091	47.62	1.50	5.96	283.95
Cephalopholis argus	Blue-spotted Grouper		0.13	0.052	71.43	0.75	3.45	246.47
Scarus psittacus	Palenose Parrotfish	*uhu*	0.25	0.044	52.38	1.50	2.91	152.39
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.06	0.034	47.62	0.36	2.23	106.35

Table 50. Top ten species in the Kailua Kona FMA, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.60	0.063	59.38	9.43	13.84	822.03
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.67	0.027	62.50	10.53	5.79	362.01
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.60	0.039	34.38	9.43	8.46	290.78
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.08	0.026	43.75	1.26	5.61	245.41
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.09	0.023	43.75	1.38	5.10	223.07
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.09	0.027	37.50	1.42	5.86	219.89
Melichthys niger	Black Durgon	*humuhumuelele*	0.06	0.019	40.63	0.94	4.16	169.15
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.50	0.010	65.63	7.78	2.12	138.95
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.12	0.040	12.50	1.81	8.76	109.48
Cephalopholis argus	Blue-spotted Grouper		0.03	0.010	28.13	0.43	2.27	63.92

Table 51. Top ten species in the Kailua Kona open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Zebrasoma flavescens	Yellow Tang	*lauipala*	1.29	0.154	100.00	9.20	16.38	1638.36
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	1.49	0.067	100.00	10.63	7.09	709.03
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	1.01	0.078	75.00	7.21	8.34	625.86
Ctenochaetus hawaiiensis	Black Surgeonfish		0.23	0.099	55.00	1.62	10.58	582.04
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.21	0.065	80.00	1.51	6.88	550.53
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.13	0.050	70.00	0.94	5.37	376.23
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.29	0.065	50.00	2.08	6.94	347.08
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.74	0.017	100.00	5.27	1.81	180.84
Chromis vanderbilti	Blackfin Chromis		5.10	0.015	80.00	36.31	1.57	125.51
Scarus psittacus	Palenose Parrotfish	*uhu*	0.12	0.023	50.00	0.85	2.42	121.00

Lapakahi MLCD and north Kohala

The north Kohala study area extended from Maka o Hule Point to Keaweula Bay (ca. 4.4km) and included the Lapakahi MLCD.

Sample allocation

A total of 54 samples were collected between July 14 and September 17, 2004 (Table 52; Fig. 79). The two levels of sampling stratification included major habitat types (CHB and UCH) and fisheries management regimes (open access and MLCD).

Table 52. Sample allocation for north Kohala study area.

Habitat	MLCD	Open	Total
Colonized hardbottom	15	13	28
Uncolonized hardbottom	13	13	26
Total	28	26	54

Large-scale benthic cover

Benthic coverage for Lapakahi MLCD derived from the NOAA benthic habitat maps consisted primarily of colonized volcanic rock/boulder (60%), aggregated coral (19%), and uncolonized volcanic rock and boulder (18%) (Table 53).

Table 53. Benthic cover for the Lapakahi MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized hardbottom	Aggregated coral	101092	18.73
	Colonized volcanic rock/boulder	323739	59.98
	Scattered coral/rock in sand	12668	2.35
Sand		3481	0.64
Uncolonized hardbottom	Uncolonized volcanic rock/boulder	98730	18.29
Grand total		539710	100.00

Small-scale benthic cover of substrate types within the management regimes.

The most abundant substrate type was turf algae, which averaged 69% cover in the MLCD and 59 % cover in the open access area (Table 54; Fig. 80). Coral cover was the next most abundant substrate with 17% in the MLCD and 21% in the open access area. *Porites lobata* and *P. compressa* were the primary coral species in both the MLCD (10% and 4%) and the open access area (17% and 2%). Other species (e.g. *Pocillopora meandrina* and *Montipora* spp.) comprised less than 3% of the remaining cover. Cover of coralline algae was higher in the open access area (14%) compared to the MLCD (10%), but the difference was not statistically significant. Cover of coralline algae was highest at Lapakahi compared to the other study sites. Sand was limited to small pockets in both the MLCD (1%) and the open access areas (2%). Macroalgae covered less than 1% of the substrate and again corresponded to an abundance of *Echinometra mathaei*.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types (Fig. 80). This result indicated that comparing fish assemblages across the management strata was appropriate at the level of major subtrate types.

<u>Fish assemblage characteristics among habitat types and between management regimes</u>
Species richness was similar within the MLCD and adjacent open areas (Fig. 81 and 84, Table 55A). Biomass (Table 55B; Fig. 82 and 85) and diversity (Table 55C, Fig. 83 and 86) were both significantly higher in the MLCD compared to open areas. There were no differences in species richness and diversity between colonized and uncolonized hardbottom habitats, but the uncolonized hardbottom open area had significantly lower biomass than the colonized open area and both habitat types within the MLCD (Table 55A, 55B, and 55C).

<u>Fish trophic structure between management regimes and among habitats</u>
Herbivores were more abundant, by weight, in the uncolonized hardbottom habitat, regardless of management regime (Fig. 87). Conversely, secondary consumers were more common in the colonized hardbottom habitats. Apex predator biomass was low overall, comprising 3% of the biomass in the MLCD and 1% in the open area. Apex predators in the MLCD were four times more abundant by weight than the open area and consisted of roi (60%) and omilu (40%).

<u>Species composition by management regime</u>
Yellow tang (*lauipala*) accounted for 17% of total fish biomass and occurred on 100% of the transects in the MLCD (Table 56). This was followed by the brown surgeonfish (maiii), which also occurred on 100% of the transects and comprised 5% of the biomass in the MLCD. In the open area, these same two species dominated but brown surgeonfish occurred on slightly more transects (96%) than the yellow tang (88%) (Table 57). Other important resource species in the MLCD included: the orangeband surgeonfish (naenae), goldring surgeonfish (*kole*), palenose parrotfish (*uhu*), and whitebar surgeonfish (*maikoiko*).

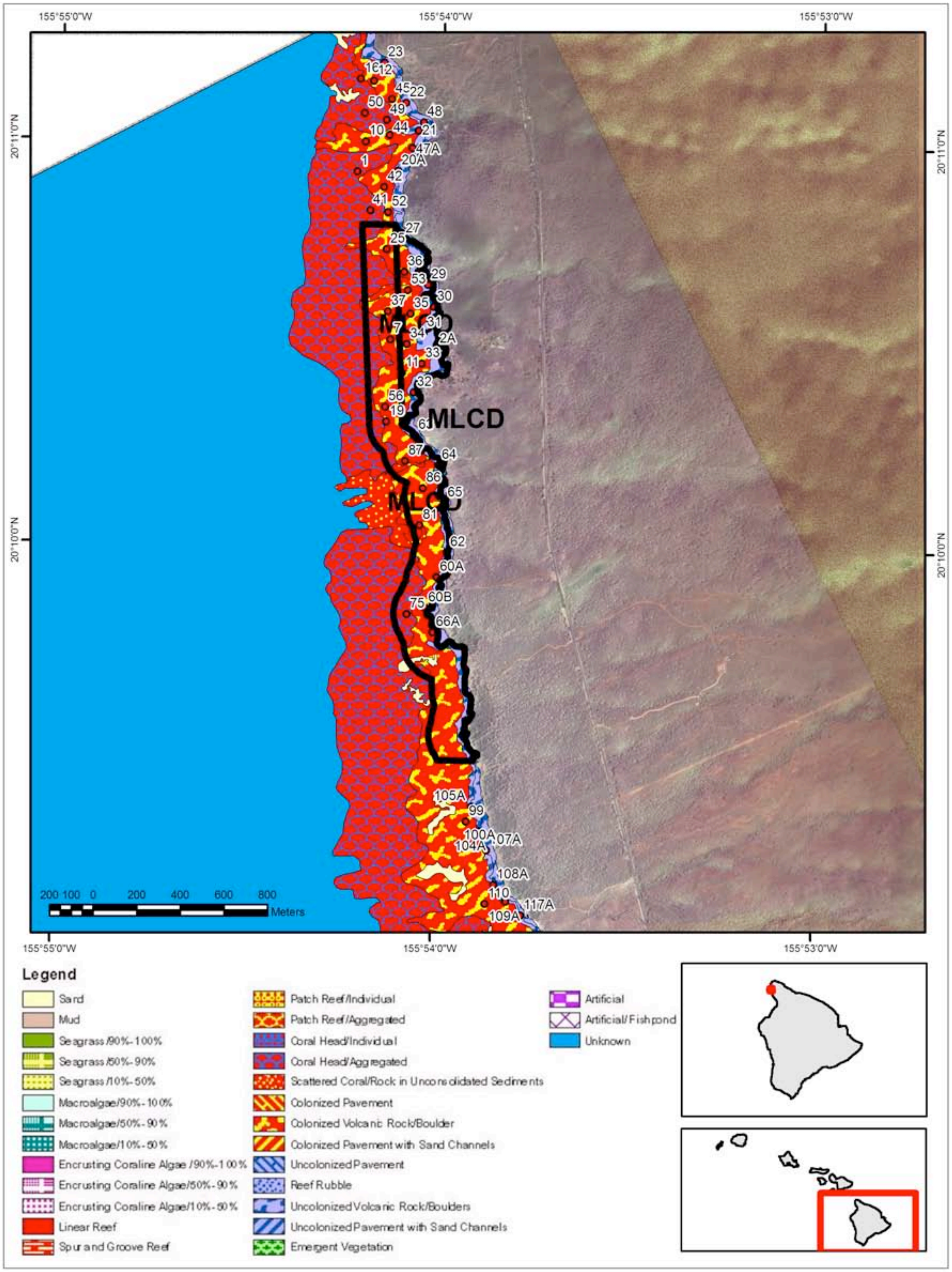

Figure 79. Sampling locations and benthic habitats for the Lapakahi MLCD and adjacent areas.

Table 54. Top 10 benthic taxa/substrate types by percent cover within the Lapakahi Marine Life Conservation District (MLCD) and the open access area outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		69.2	Turf algae		59.3
Coral	*Porites lobata*	10.3	Coral	*Porites lobata*	16.8
Coralline algae		10.2	Coralline algae		14.4
Coral	*Porites compressa*	4.4	Coral	*Porites compressa*	2.3
Sand		1.3	Sand		2.2
Macroinvertebrate	*Echinometra mathaei*	1.3	Macroinvertebrate	*Echinometra mathaei*	2.0
Coral	*Pocillopora meandrina*	1.2	Coral	*Pocillopora meandrina*	0.8
Coral	*Montipora capitata*	0.8	Coral	*Montipora patula*	0.5
Macroalgae	*Hormothamnion sp.*	0.3	Coral	*Montipora capitata*	0.3
Macroinvertebrate	*Echinothrix calamaris*	0.2	Coral	*Porites evermanni*	0.3

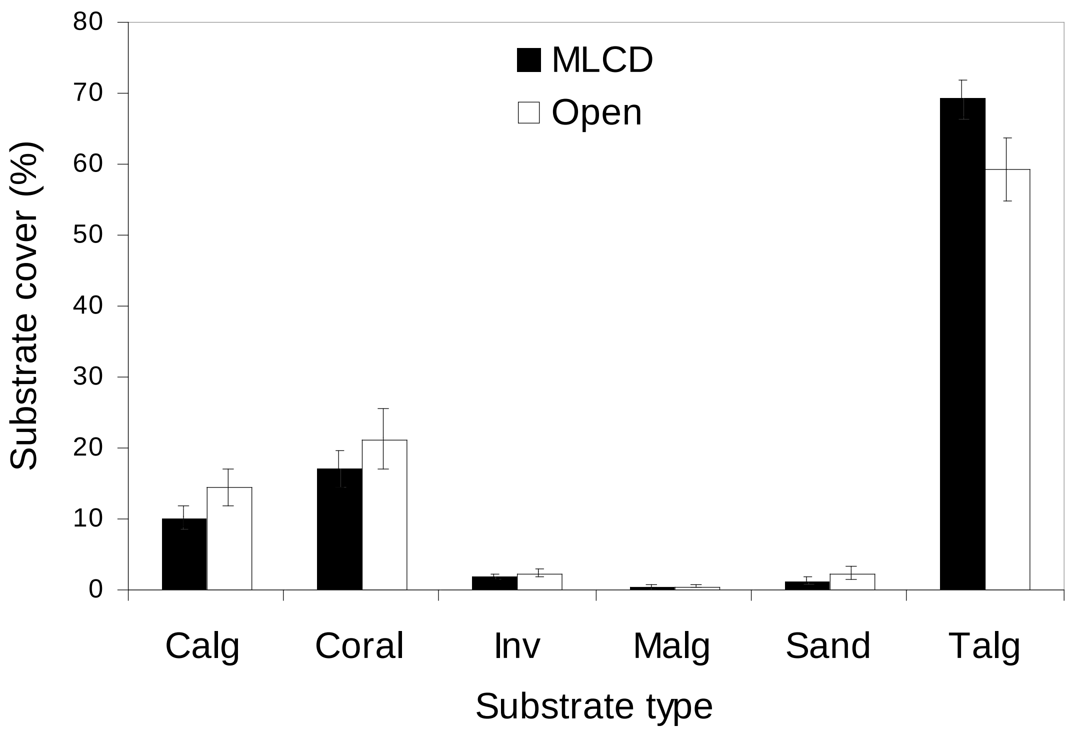

Figure 80. Mean percent cover of substrate types within the Lapakahi Marine Life Conservation District (MLCD) and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

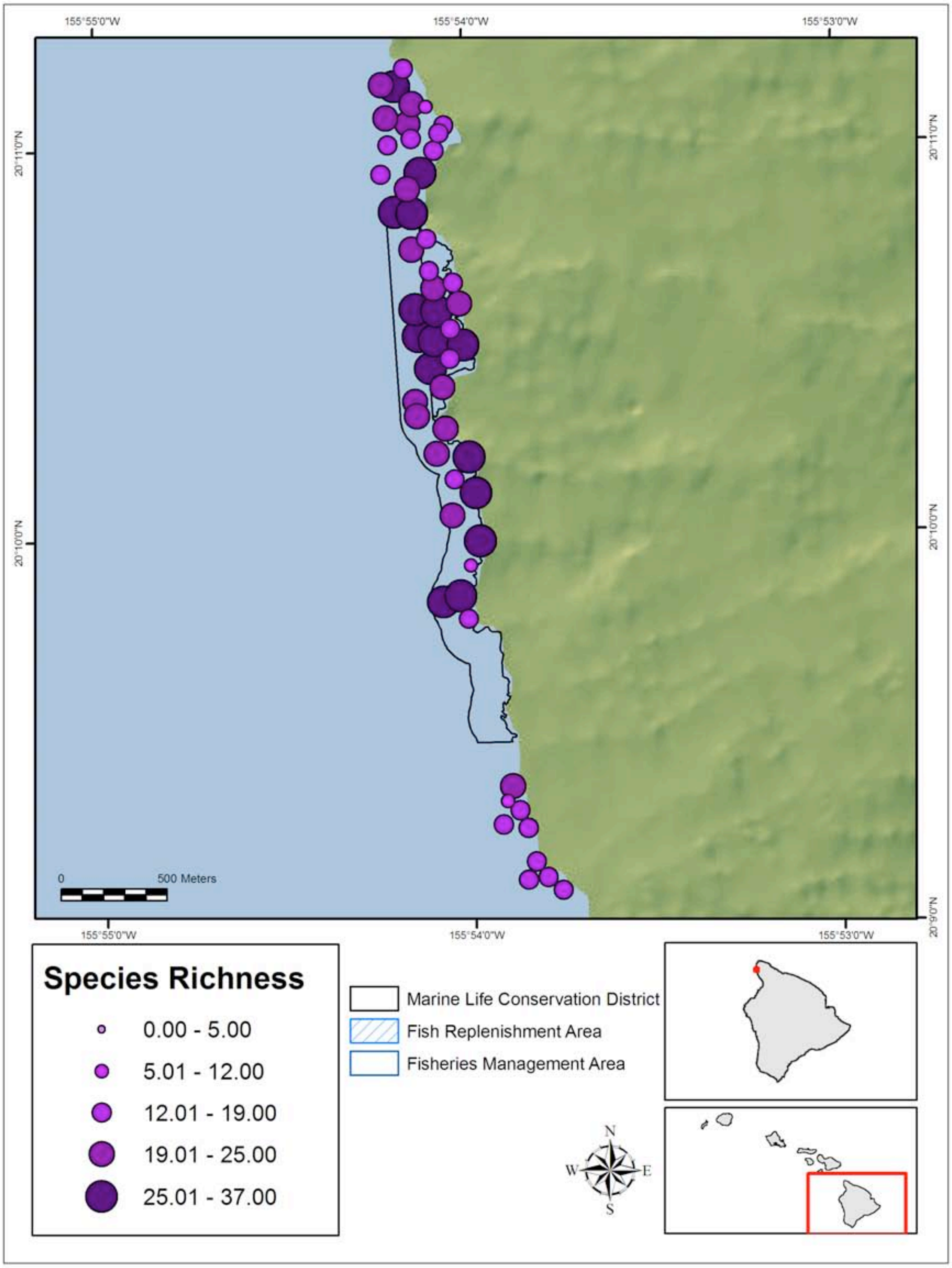

Figure 81. Species richness by individual transects (N=54) for the north Kohala study area, including Lapakahi MLCD. Classification based on quantiles.

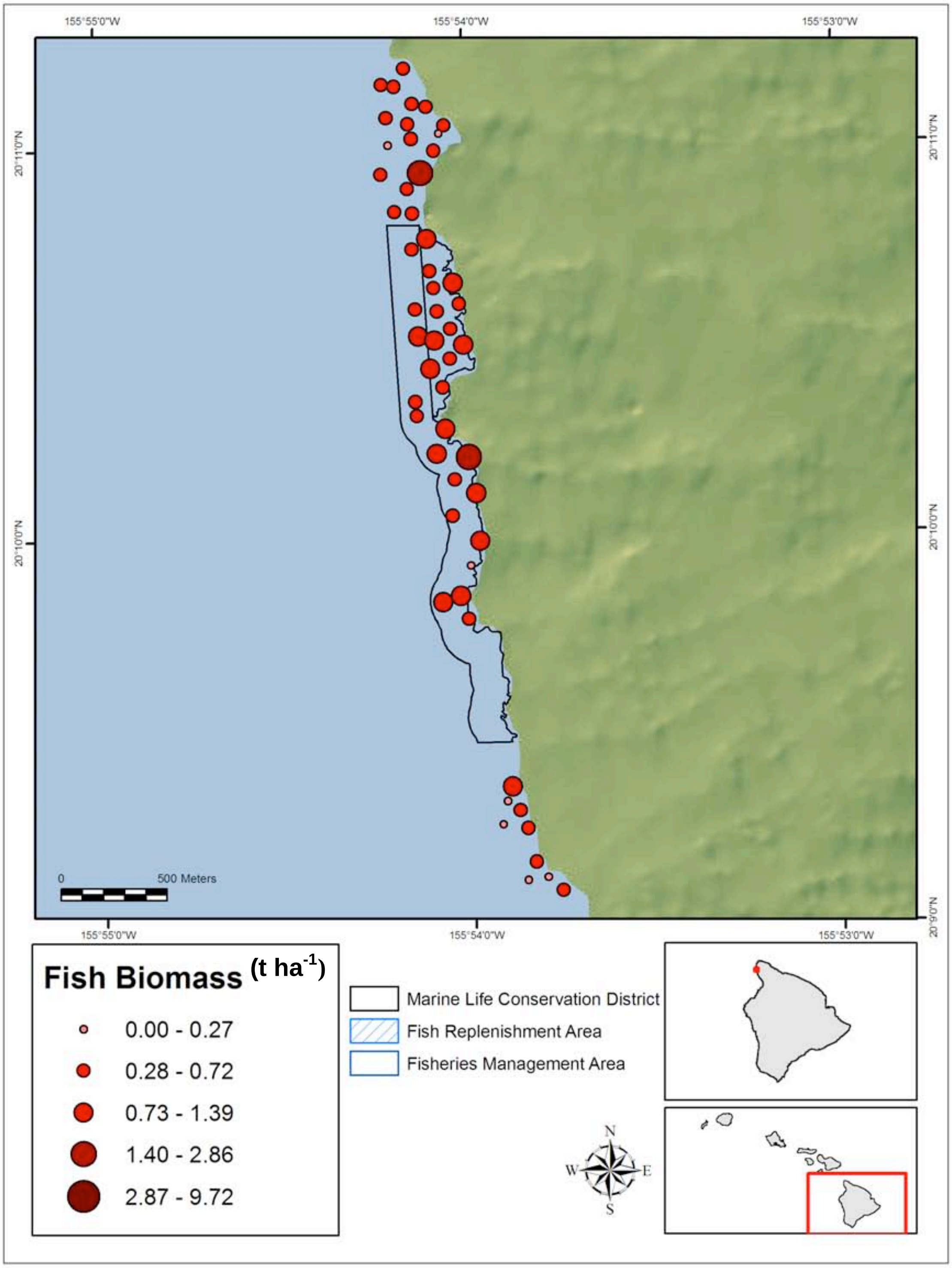

Figure 82. Fish biomass (t ha^{-1}) by individual transects (N=54) for the north Kohala study area, including Lapakahi MLCD. Classification based on quantiles.

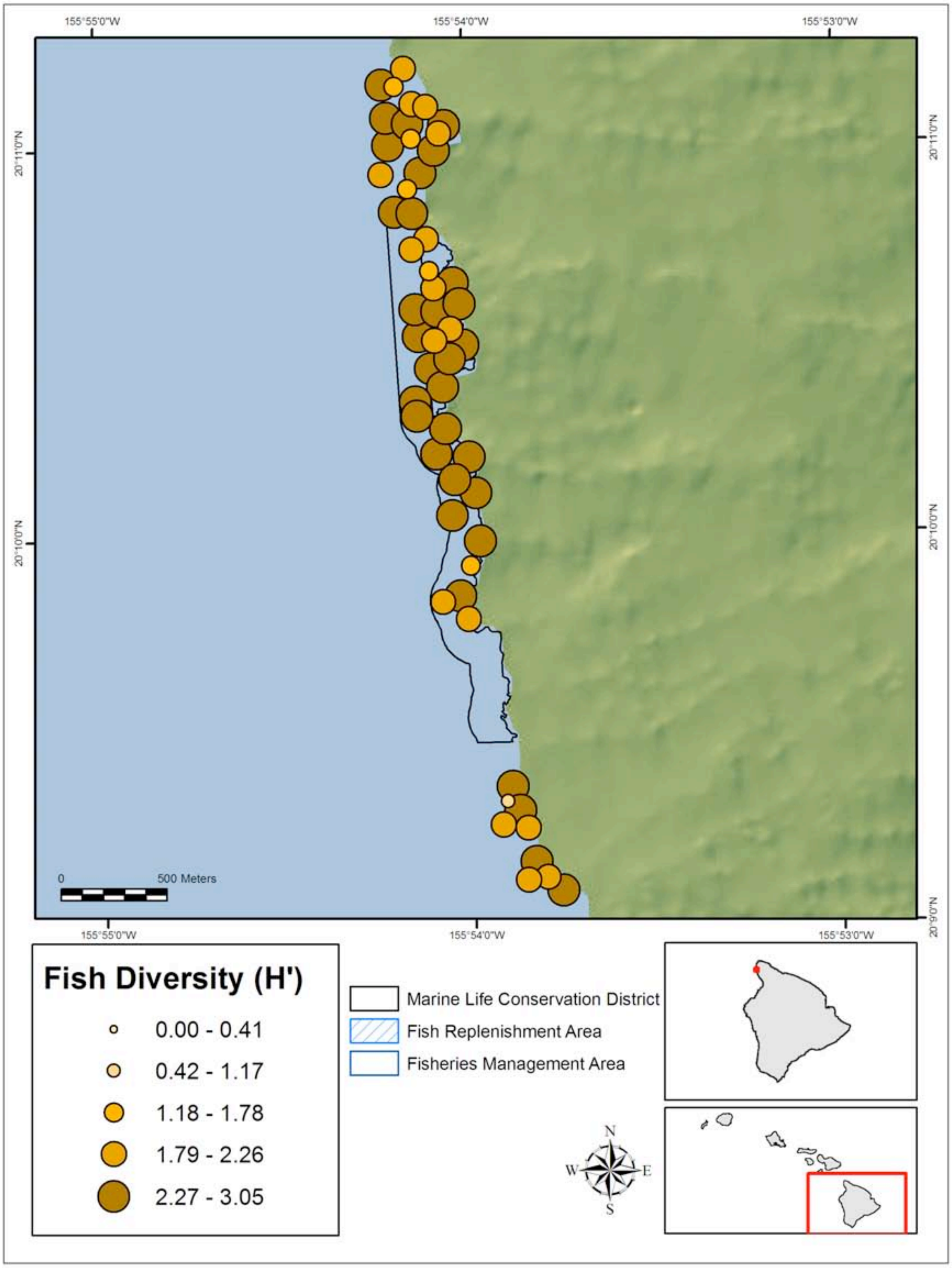

Figure 83. Fish diversity (H') by individual transects (N=54) for the north Kohala study area, including Lapakahi MLCD. Classification based on quantiles.

Table 55A. Comparison of fish species richness among management regimes and habitat types for the north Kohala study area. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 54). Management regimes: MLCD ([M]) and Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB) and <10% live coral hard bottom (UCH). Unplanned multiple comparisons among management strata and habitat$_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different ($\alpha = 0.05$)

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	80.9	2.78	0.051	
Management	1	169.8	5.83	0.019	MLCD = Open
Habitat$_{[management]}$	2	33.5	1.15	0.325	
Error	50	29.1			
Habitat$_{[management]}$ -					CHB$_{[M]}$ UCH$_{[M]}$ CHB$_{[O]}$ UCH $_{[O]}$

Table 55B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the north Kohala study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	0.20	5.95	0.002	
Management	1	0.38	11.37	0.001	MLCD > Open
Habitat$_{[management]}$	2	0.12	3.57	0.035	
Error	50	0.03			
Habitat$_{[management]}$ -					UCH$_{[M]}$ CHB$_{[M]}$ CHB$_{[O]}$ UCH $_{[O]}$

Table 55C. Comparison of fish species diversity (H') among management regimes and habitat types for the north Kohala study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	0.25	2.05	0.119	
Management	1	0.51	4.08	0.049	MLCD > Open
Habitat$_{[management]}$	2	0.14	1.10	0.339	
Error	50	0.12			
Habitat$_{[management]}$ -					UCH$_{[M]}$ CHB$_{[M]}$ UCH$_{[O]}$ CHB$_{[O]}$

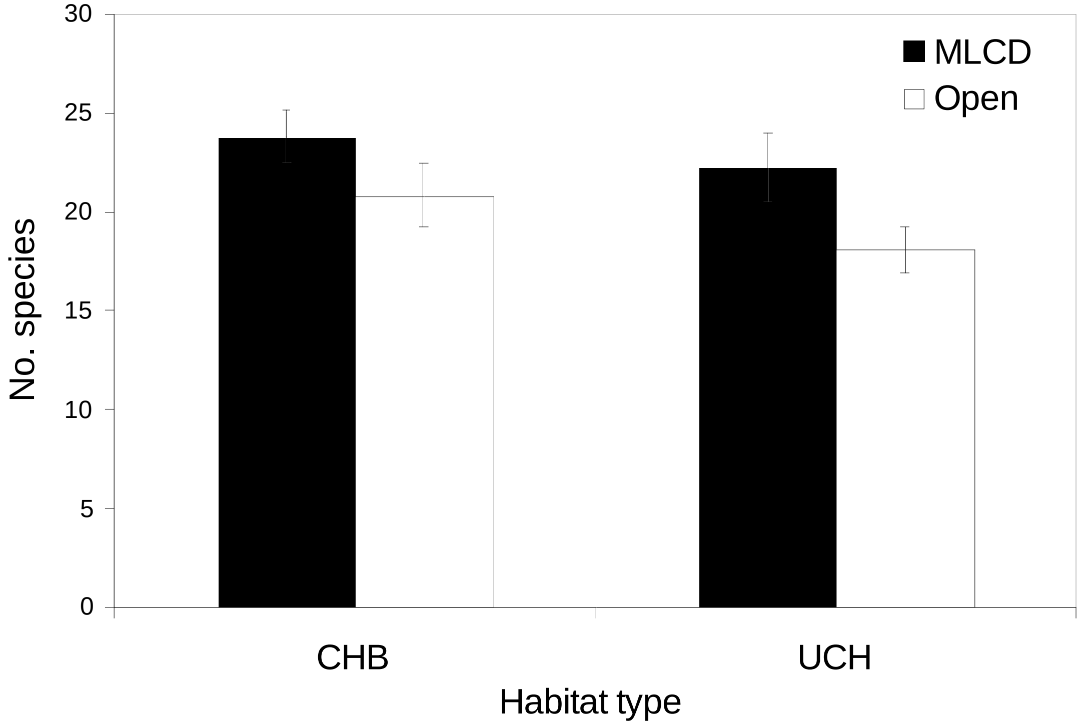

Figure 84. Mean number of species per transect (125 m^2) by habitat type and management regime for the north Kohala study area. Error bars are standard error of the mean.

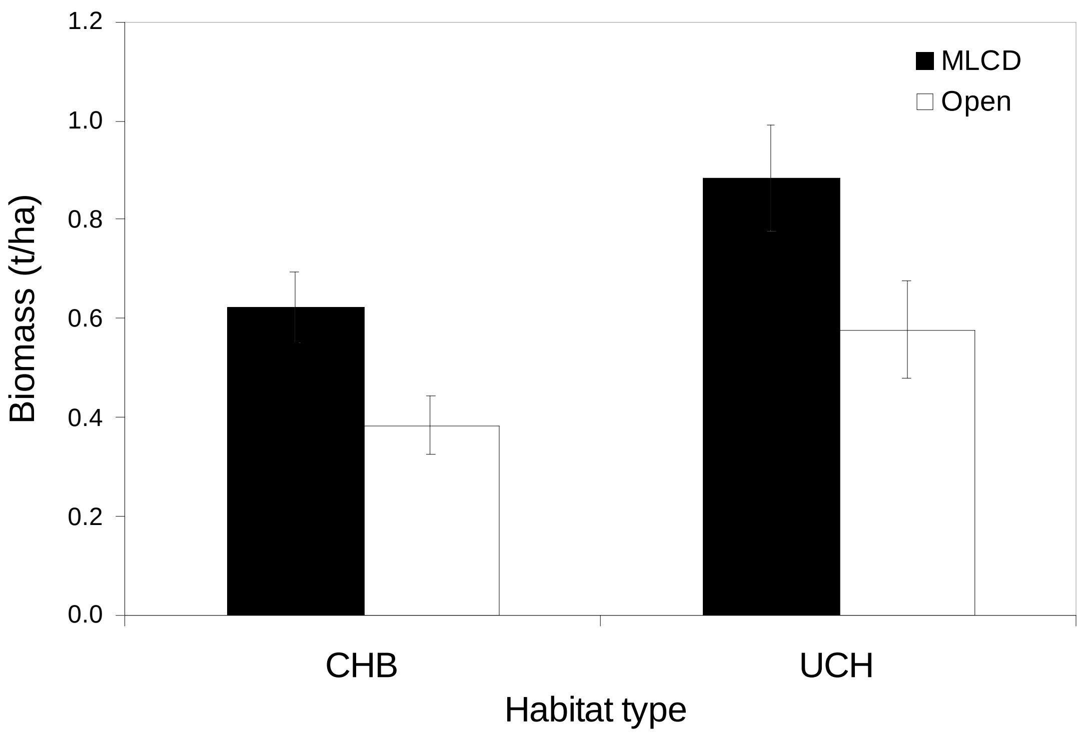

Figure 85. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the north Kohala study area. Error bars are standard error of the mean.

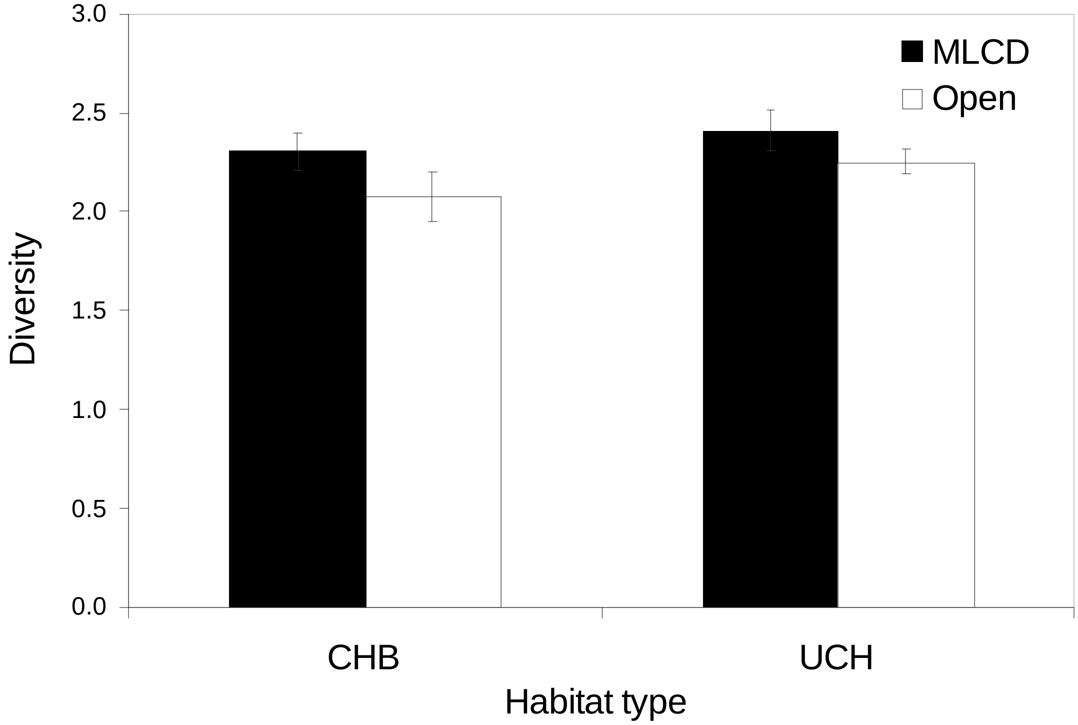

Figure 86. Mean diversity (H’) per transect (125 m^2) by habitat type and management regime for the north Kohala study area. Error bars are standard error of the mean

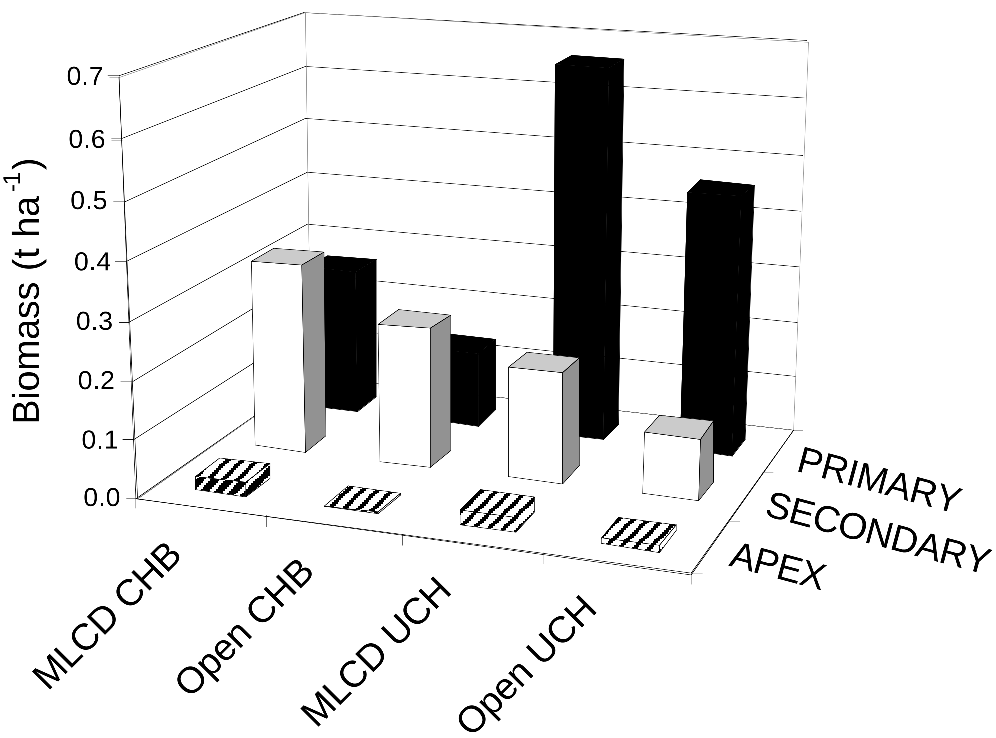

Figure 87. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the north Kohala study area.

Table 56. Top ten species in the Lapakahi MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Zebrasoma flavescens	Yellow Tang	*lauipala*	1.11	0.125	100.00	10.00	16.77	1677.07
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	1.32	0.041	100.00	11.88	5.55	554.95
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.18	0.053	60.71	1.60	7.11	431.69
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.95	0.049	64.29	8.58	6.52	419.45
Scarus psittacus	Palenose Parrotfish	*uhu*	0.14	0.043	57.14	1.24	5.73	327.59
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.24	0.057	32.14	2.19	7.60	244.35
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.70	0.015	100.00	6.34	1.98	198.24
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.08	0.027	53.57	0.72	3.56	190.96
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.11	0.014	78.57	1.03	1.86	146.15
Bodianus bilunulatus	Hawaiian Hogfish	*aawa*	0.05	0.024	35.71	0.44	3.29	117.48

Table 57. Top ten species in the north Kohala open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	1.53	0.052	96.15	15.99	10.76	1034.32
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.54	0.052	88.46	5.61	10.80	955.82
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.93	0.043	57.69	9.77	8.85	510.70
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.37	0.062	30.77	3.87	12.99	399.75
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.09	0.020	53.85	0.90	4.23	227.93
Melichthys niger	Black Durgon	*humuhumuelele*	0.08	0.038	23.08	0.87	7.94	183.24
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.50	0.010	88.46	5.26	2.05	181.68
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.11	0.012	65.38	1.13	2.57	168.31
Scarus psittacus	Palenose Parrotfish	*uhu*	0.06	0.021	26.92	0.68	4.46	119.98
Parupeneus multifasciatus	Manybar Goatfish	*moano*	0.14	0.007	73.08	1.48	1.53	111.93

WaiOpae MLCD and Kapoho area

The Kapoho study area extended from Kapoho Point to Hale Point (ca. 1.2km) and included the WaiOpae MLCD. This unique habitat consisted of a series of tidepools on a raised lava bench.

Sample allocation

A total of 57 samples were collected between November 30 and December 19, 2004 (Table 58; Fig. 88). The two levels of sampling stratification included major habitat types (CHB and UCH) and fisheries management regimes (open access and MLCD).

Table 58. Sample allocation for Kapoho study area.

Habitat	MLCD	Open	Total
Colonized hardbottom	14	14	28
Uncolonized hardbottom	15	14	29
Total	29	28	57

Large-scale benthic cover

Benthic coverage for WaiOpae MLCD derived from the NOAA benthic habitat maps consisted primarily of unknown optically deep water seaward of the reef crest (40%). Of the remaining habitat, 13% consisted of uncolonized volcanic rock w/ coralline algae, 12% consisted of uncolonized volcanic rock/boulder, 12% consisted of colonized volcanic rock, and 11% consisted of algal plain (Table 59).

Table 59. Benthic cover for the WaiOpae MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized bedrock	Colonized volcanic rock	23249	11.71
Macroalgae	Algal plain	21675	10.92
Patch reef (Aggregated)	Patch reef	18998	9.57
Reef rubble	Reef rubble with turf	4854	2.44
Uncolonized volcanic rock	Uncolonized volcanic rock w/ coralline algae	26613	13.40
	Uncolonized volcanic rock w/ emergent vegetation	1339	0.67
Uncolonized volcanic rock/boulder		23643	11.91
Unknown (optically deep water)		78196	39.38
Grand Total		198566	100.00

Small-scale benthic cover of substrate types within the management regimes.

The most abundant substrate type was turf algae, which averaged 56% cover in the MLCD and 60 % cover in the open access area (Table 60; Fig. 89). Macroalgae in the MLCD covered 18%, which was attributed to the abundance of Cyanobacteria (9%), *Laurencia sp.* (2%), *Schizothrix sp.* (2%), and *Dictyota sp.* (2%). In comparison, macroalgal cover in the open access area was 15%, but was composed primarily of *Dictyota sp.* (8%) with lower levels of Cyanobacteria (2%), *Ralfsia sp.* (1%), and *Melanamansia sp.* (1%). Coral cover was similar to macroalgal cover, with 17% in the MLCD and 15% in the open access area. *Montipora capitata* and *Porites lobata* were the primary coral species in the MLCD (7% and 5%). In contrast, *M. capitata* cover in the open access area was <1% while *P. lobata* (9%) and *Pocillopora meandrina* (3%) were the predominant corals. Cover of coralline algae was higher in the open access area (10%) compared to the MLCD (6%), but the difference was not statistically significant. Sand cover was minimal in both the MLCD (2%) and the open access areas (<1%). The remaining macroinvertebrates and coralline algae were less than 1% of the benthic cover.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types (Fig. 89). This result indicated that comparing fish assemblages across the management strata was appropriate at the level of major subtrate types.

Fish assemblage characteristics among habitat types and between management regimes

Species richness (Fig. 90) and diversity (Fig. 92) were similar between the MLCD and the adjacent habitat (Table 61A and 61C), while biomass (Fig. 91) was significantly higher in the MLCD (Table 61B). The colonized hardbottom habitats had the highest values for richness and diversity, while biomass estimates did not differ significantly between habitat types. (Table 61A, 61B, and 61C; Fig. 93, 94, and 95).

Fish trophic structure between management regimes and among habitats

Trophic structure in the MLCD consisted of 64% herbivores, 34% secondary consumers, and less than 2% apex predators (primarily the introduced peacock grouper, roi) (Fig. 96). In the open area, herbivores comprised 55% of the biomass, followed by secondary consumers (44%), and less than 1% apex predators. In the MLCD, herbivores were twice as abundant by weight in the colonized habitat compared to the uncolonized habitat, while in the open area herbivores were slightly more abundant in the uncolonized habitat.

Species composition by management regime

Although the majority of the species observed in the tidepools were small or juveniles of larger species, there were a few important resource species observed, particularly in the MLCD. The palenose parrotfish (*uhu*) and convict tang (*manini*) were the two most dominant species in the MLCD, based on IRD, and accounted for 35% of the biomass in this management stratum (Table 62). These two species comprised 25% of the biomass in the open area but were not as important based on IRD (Table 63). The keeltail needlefish (*aha*, *Platybelone argalus*) was observed on 20% of the transects in the MLCD and accounted for 5% of the biomass.

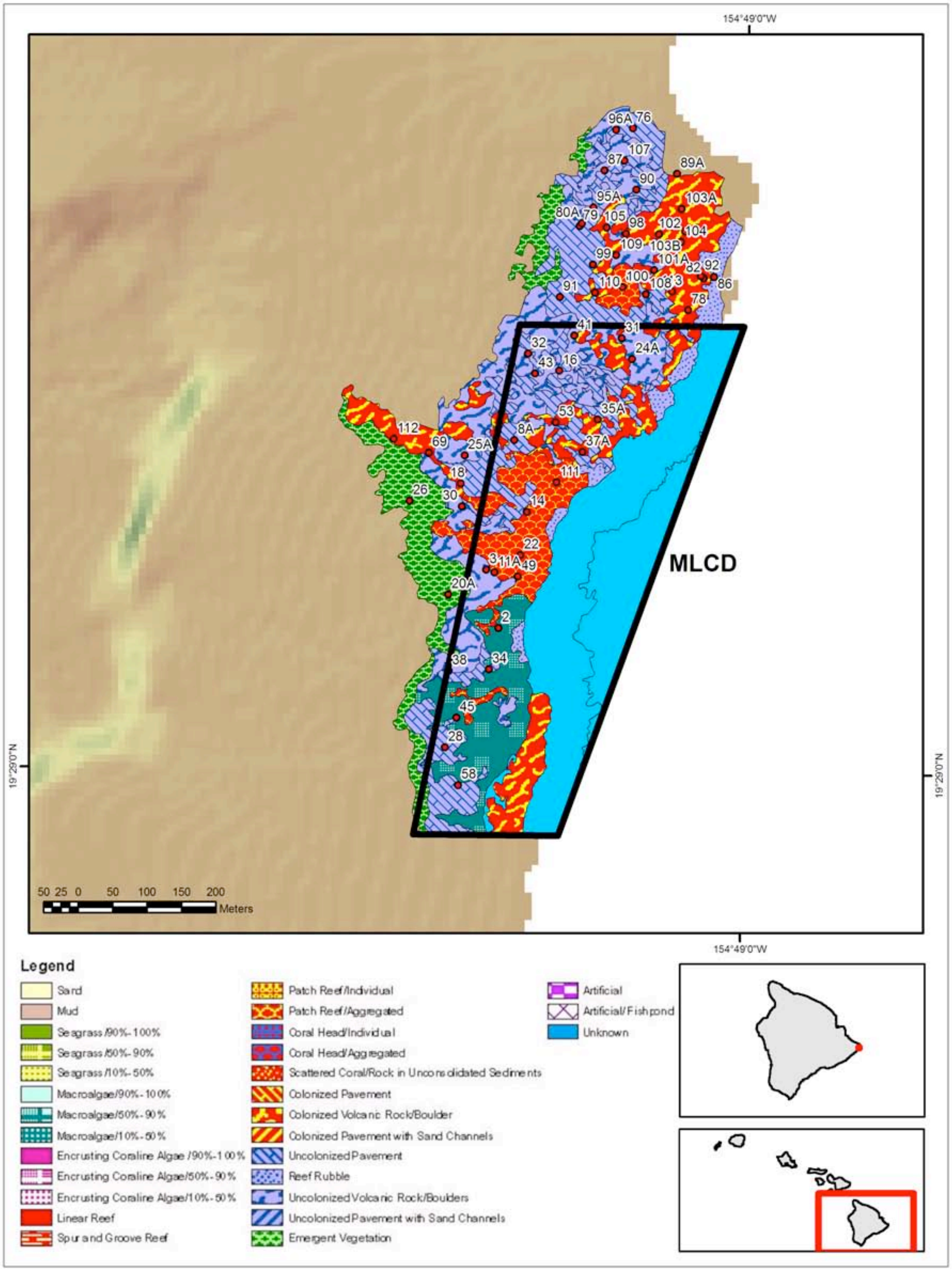

Figure 88. Sampling locations and benthic habitats for the WaiOpae MLCD and adjacent areas. Western boundary of MLCD extends landward to the highwater mark at the shoreline (HAR 13-38).

Table 60. Top 10 benthic taxa/substrate types by average percent cover within the WaiOpae Marine Life Conservation District (MLCD) and the open access area outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		56.3	Turf algae		59.9
Macroalgae	Cyanobacteria	8.9	Coralline algae		9.8
Coral	*Montipora capitata*	7.4	Coral	*Porites lobata*	8.5
Coralline algae		5.9	Macroalgae	*Dictyota sp.*	8.3
Coral	*Porites lobata*	4.5	Coral	*Pocillopora meandrina*	2.5
Sand		1.8	Macroalgae	Cyanobacteria	2.0
Macroalgae	*Laurencia sp.*	1.7	Macroalgae	*Ralfsia sp.*	1.0
Macroalgae	*Schizothrix sp.*	1.5	Coral	*Montipora patula*	1.0
Macroalgae	*Dictyota sp.*	1.5	Macroalgae	*Melanamansia sp.*	0.8
Coral	*Montipora patula*	1.1	Coral	*Pavona varians*	0.7

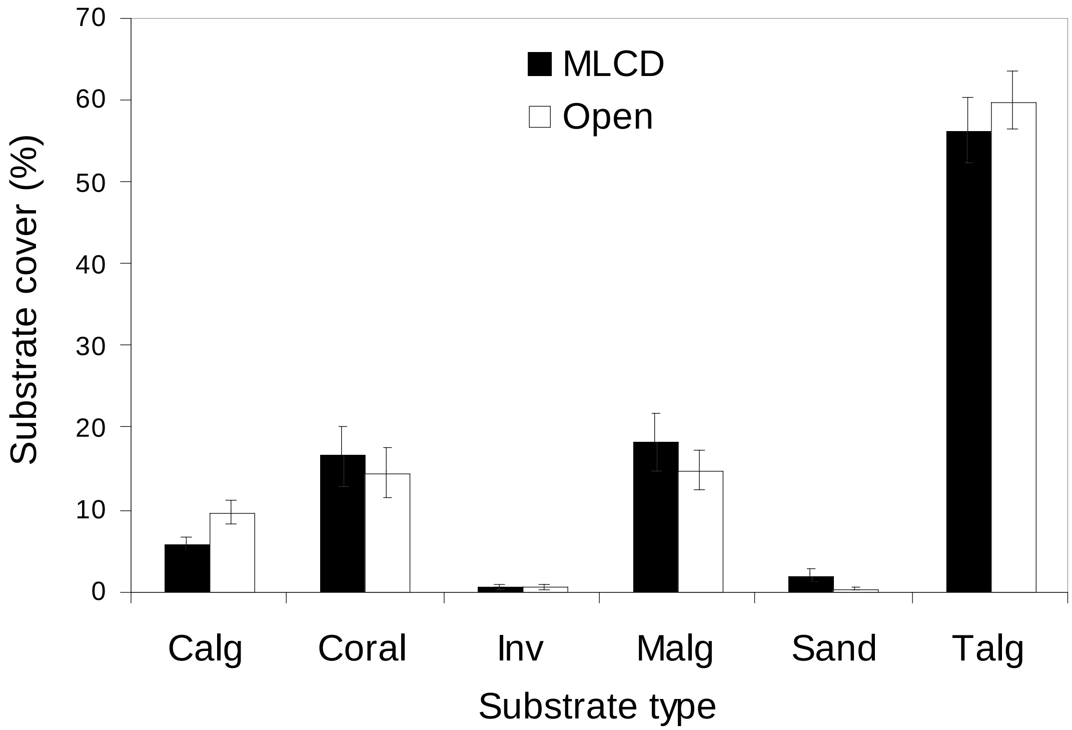

Figure 89. Mean percent cover of substrate types within the WaiOpae Marine Life Conservation District (MLCD), and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand and Bare Rock, Talg = Turf algae. Error bars are ± 1 SE of the mean.

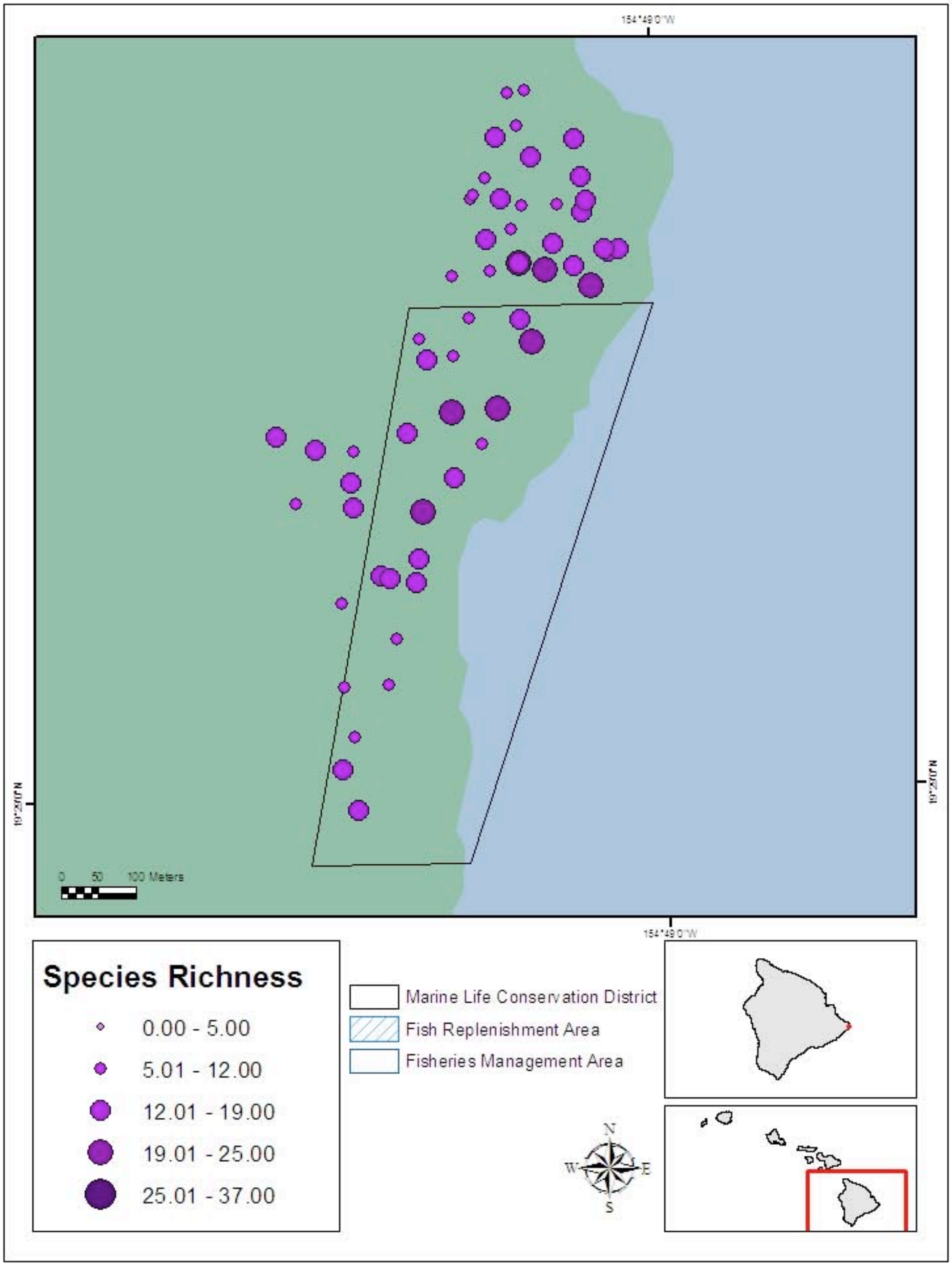

Figure 90. Species richness by individual transects (N=57) for the Kapoho study area, including WaiOpae MLCD. Classification based on quantiles. Western boundary of MLCD extends landward to the highwater mark at the shoreline (HAR 13-38).

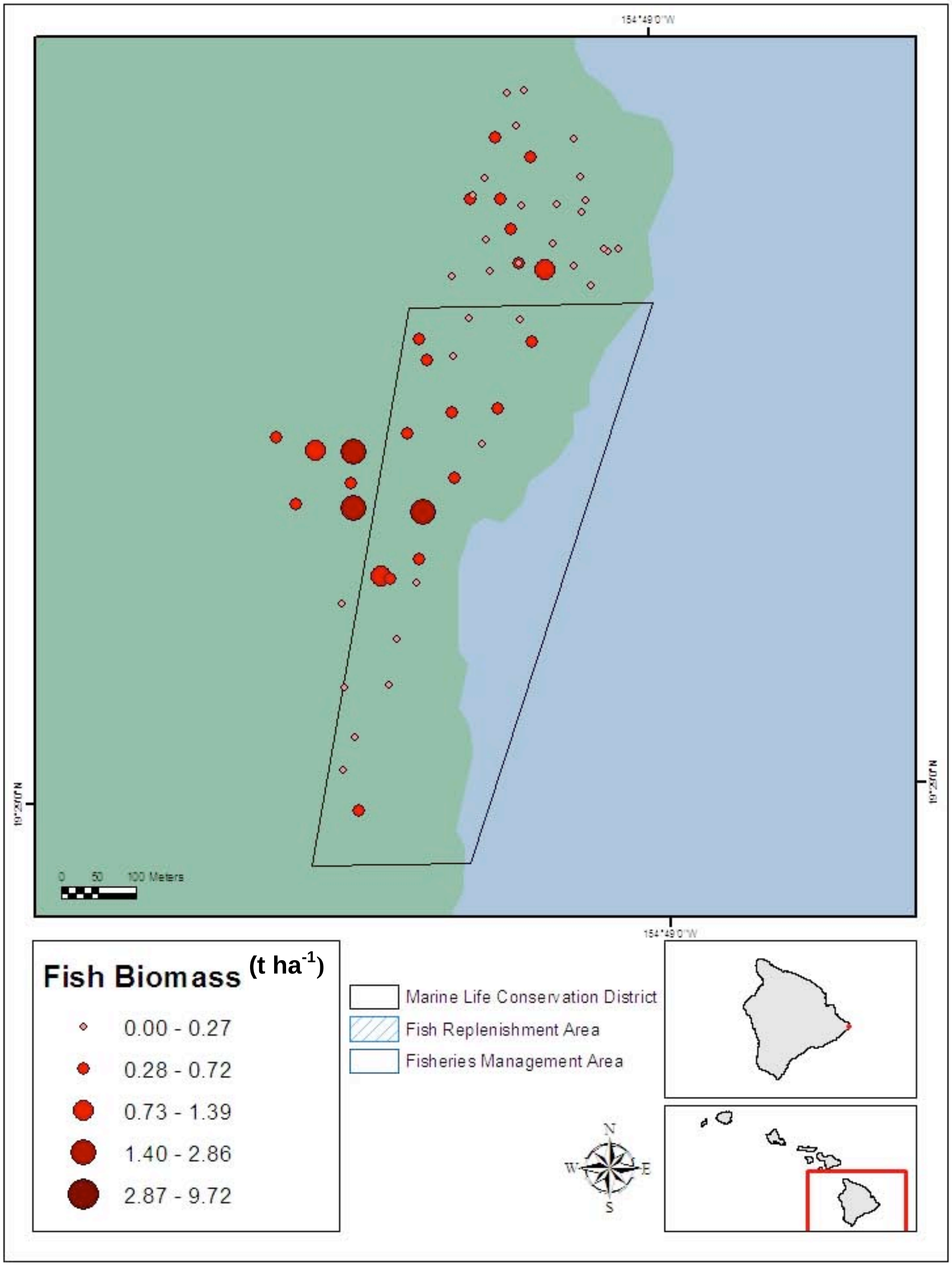

Figure 91. Fish biomass (t ha^{-1}) by individual transects (N=57) for the Kapoho study area, including WaiOpae MLCD. Classification based on quantiles. Western boundary of MLCD extends landward to the highwater mark at the shoreline (HAR 13-38).

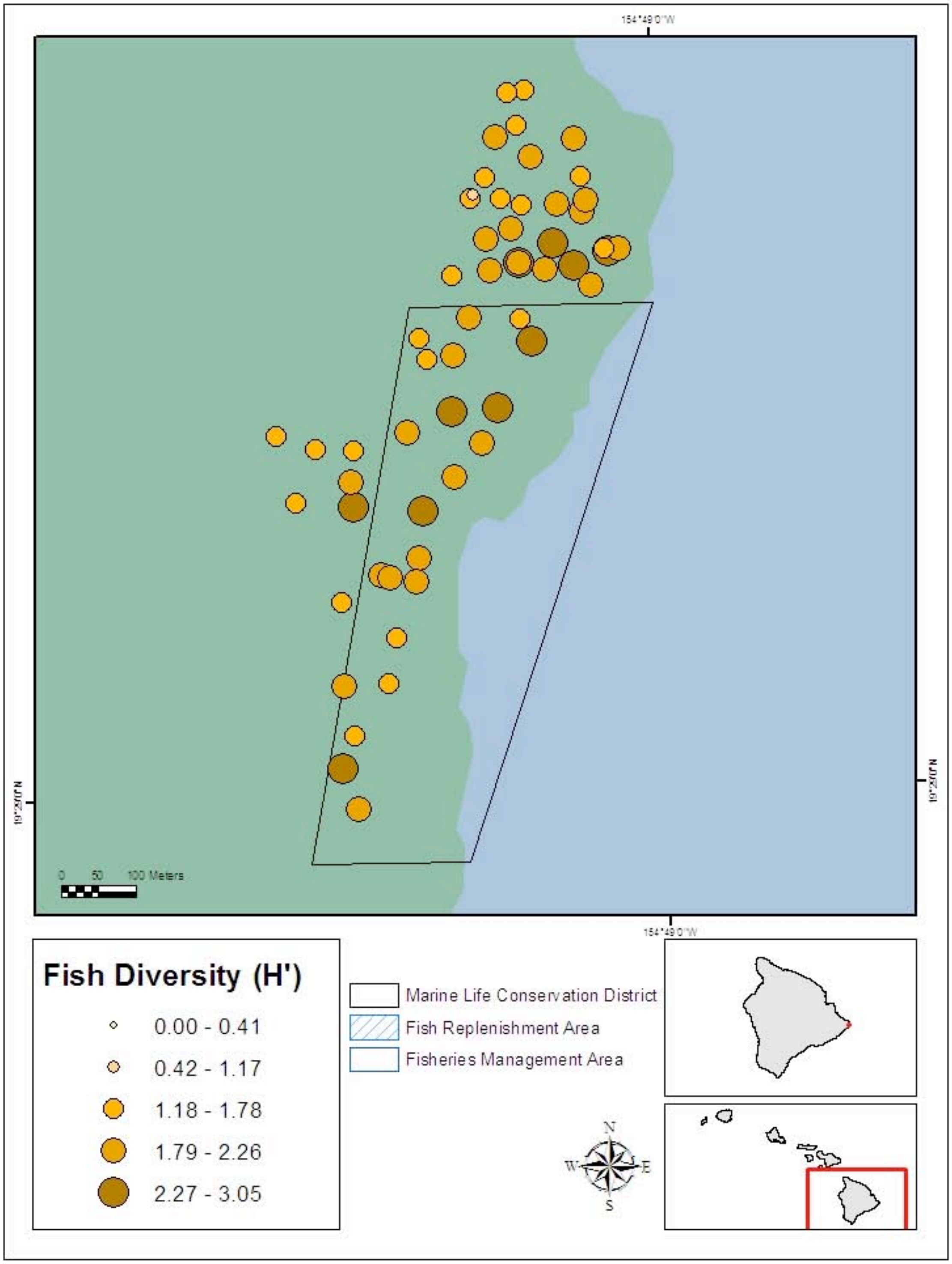

Figure 92. Fish diversity (H') by individual transects (N=57) for the Kapoho study area, including WaiOpae MLCD. Classification based on quantiles. Western boundary of MLCD extends landward to the highwater mark at the shoreline (HAR 13-38).

Table 61A. Comparison of fish species richness among management regimes and habitat types for the Kapoho study area. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 57). Management regimes: MLCD ([M]) and Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB) and <10% live coral hard bottom (UCH). Unplanned multiple comparisons among management strata and habitat$_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different (α = 0.05)

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	164.4	16.0	<0.001	
Management	1	4.8	0.5	0.500	MLCD = Open
Habitat$_{[management]}$	2	245.1	23.8	<0.001	
Error	53	10.3			
Habitat$_{[management]}$ -					$CHB_{[M]}$ $CHB_{[O]}$ $UCH_{[O]}$ $UCH_{[M]}$

Table 61B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types for the Kapoho study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	0.16	3.75	0.02	
Management	1	0.26	5.85	0.02	MLCD > Open
Habitat$_{[management]}$	2	0.12	2.83	0.07	
Error	53	0.04			
Habitat$_{[management]}$ -					$CHB_{[M]}$ $UCH_{[M]}$ $CHB_{[O]}$ $UCH_{[O]}$

Table 61C. Comparison of fish species diversity (H') among management regimes and habitat types for the Kapoho study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	3	0.58	6.66	<0.001	
Management	1	0.08	0.91	0.344	MLCD = Open
Habitat$_{[management]}$	2	0.84	9.60	<0.001	
Error	53	0.08			
Habitat$_{[management]}$ -					$CHB_{[M]}$ $CHB_{[O]}$ $UCH_{[M]}$ $UCH_{[O]}$

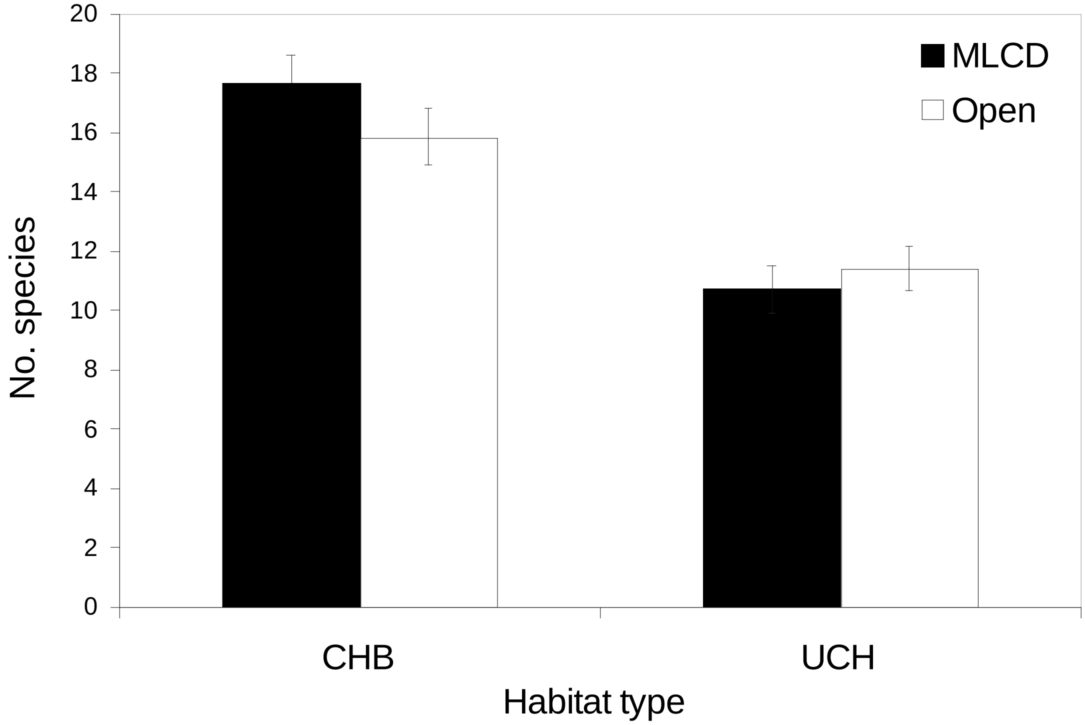

Figure 93. Mean number of species per transect (125 m^2) by habitat type and management regime for the Kapoho study area. Error bars are standard error of the mean.

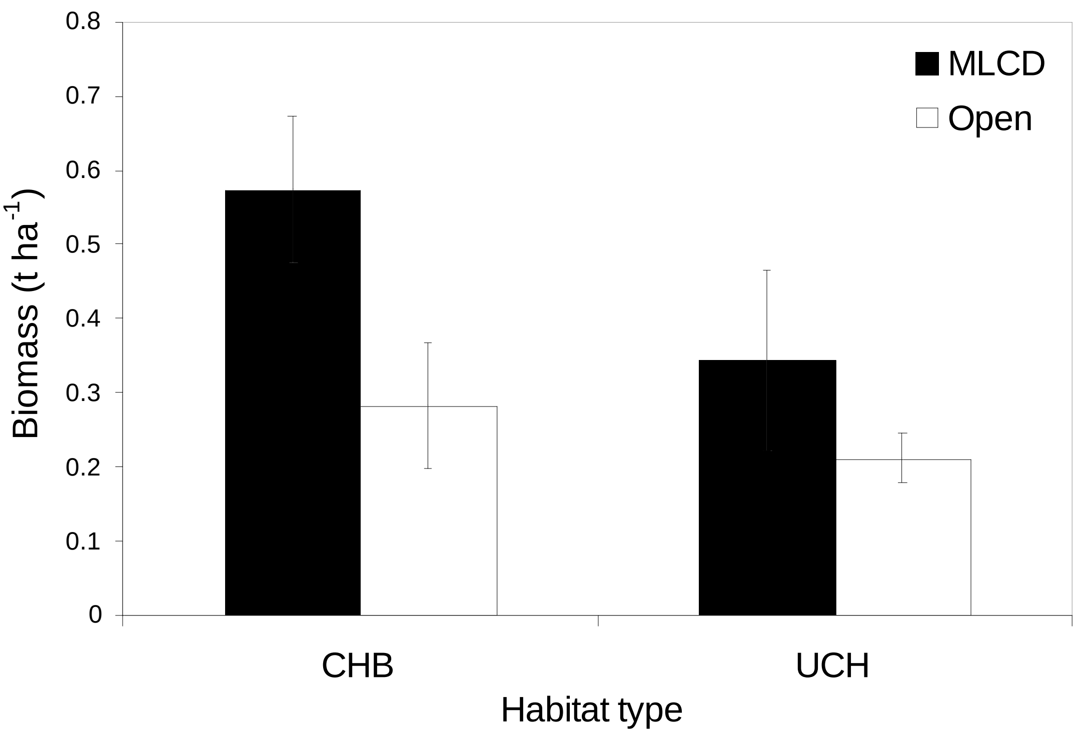

Figure 94. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the Kapoho study area. Error bars are standard error of the mean.

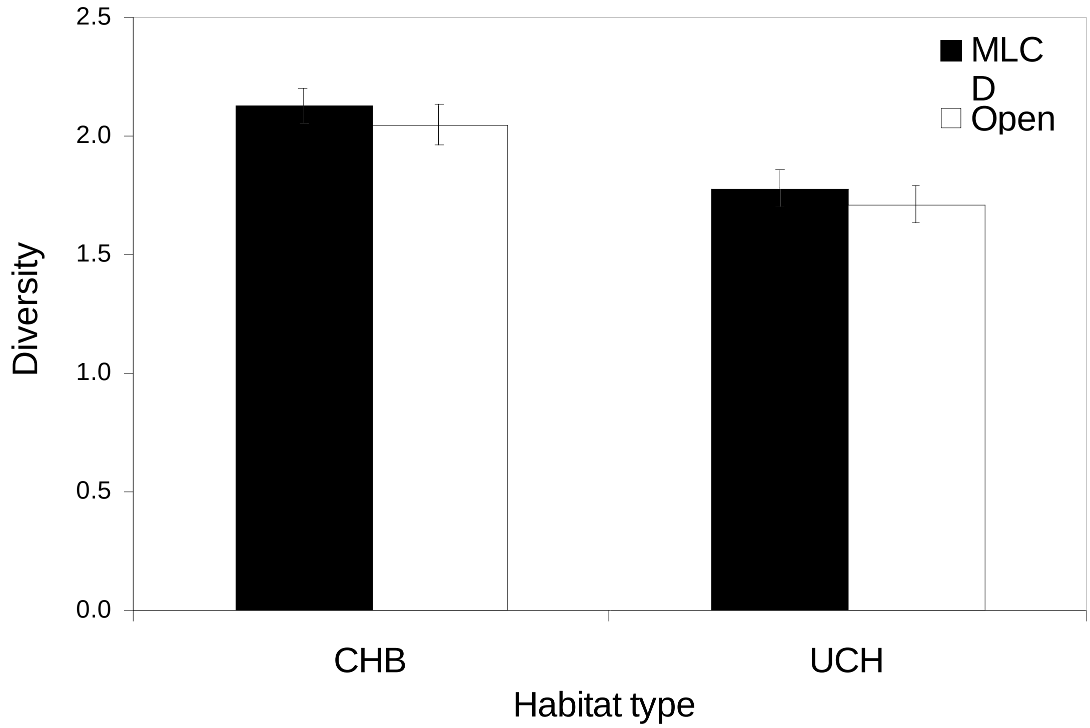

Figure 95. Mean diversity (H’) per transect (125 m^2) by habitat type and management regime for the Kapoho study area. Error bars are standard error of the mean

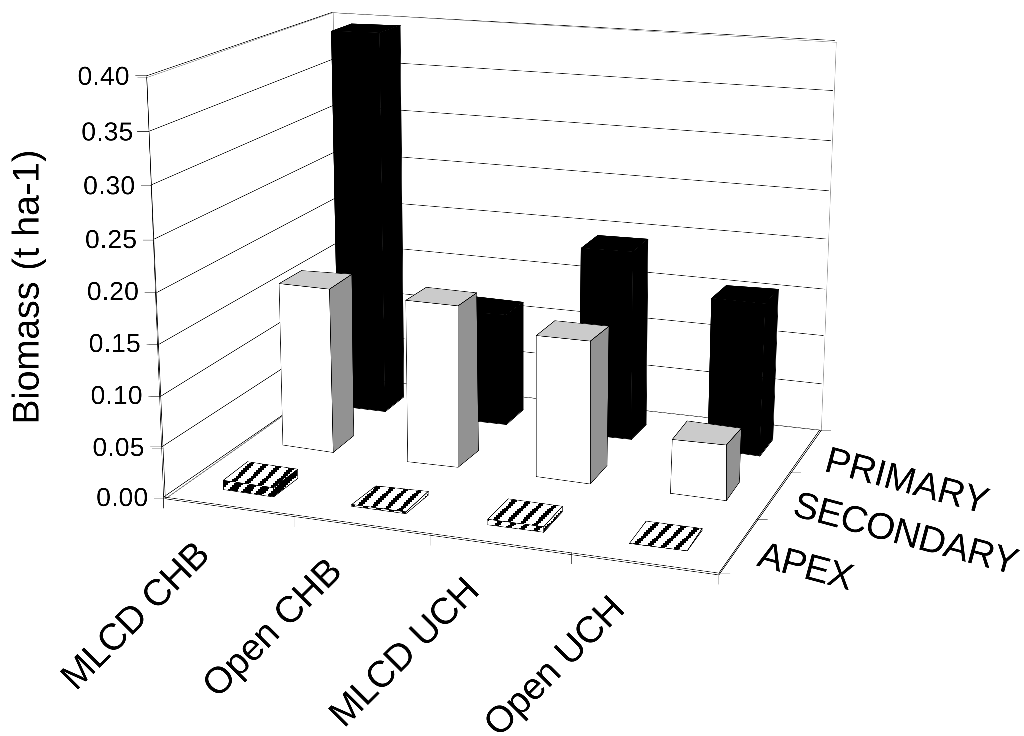

Figure 96. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the Kapoho study area.

Table 62. Top ten species in the WaiOpae MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Scarus psittacus	Palenose Parrotfish	*uhu*	1.22	0.098	75.86	15.15	21.44	1626.73
Acanthurus triostegus	Convict Tang	*manini*	1.32	0.065	86.21	16.41	14.24	1227.63
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	1.45	0.020	100.00	18.02	4.32	431.90
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.06	0.028	27.59	0.79	6.23	171.96
Stegastes fasciolatus	Pacific Gregory		0.41	0.008	82.76	5.09	1.83	151.10
Chaetodon lunula	Raccoon Butterflyfish	*kikakapu*	0.22	0.010	58.62	2.74	2.20	128.88
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.24	0.013	44.83	2.97	2.86	128.41
Platybelone argalus	Keeltail Needlefish	*aha*	0.40	0.026	20.69	4.92	5.81	120.28
Kyphosus species	Lowfin Chub	*nenue*	0.07	0.031	13.79	0.82	6.71	92.49
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.40	0.007	51.72	4.92	1.63	84.05

Table 63. Top ten species in the Kapoho open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.96	0.047	82.14	11.01	18.86	1549.09
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	2.18	0.025	100.00	25.04	10.13	1013.44
Chromis vanderbilti	Blackfin Chromis		1.20	0.043	42.86	13.80	17.35	743.56
Scarus psittacus	Palenose Parrotfish	*uhu*	0.83	0.030	60.71	9.60	11.98	727.31
Acanthurus triostegus	Convict Tang	*manini*	0.84	0.033	50.00	9.66	13.19	659.50
Stegastes fasciolatus	Pacific Gregory		0.43	0.009	75.00	5.00	3.54	265.37
Chaetodon quadrimaculatus	Fourspot Butterflyfish	*lau hau*	0.07	0.005	42.86	0.76	1.86	79.68
Gomphosus varius	Bird Wrasse	*hinalea iiwi, akilolo*	0.31	0.002	82.14	3.58	0.90	73.99
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.25	0.004	39.29	2.89	1.56	61.26
Stethojulis balteata	Belted Wrasse	*omaka*	0.17	0.002	75.00	1.91	0.79	59.49

Waialea Bay MLCD and south Kohala
The south Kohala study area extended from Kaaha Point to Puako Bay (4.7km) and included the Waialea Bay MLCD.

Sample allocation
A total of 80 samples were collected between June 14 and July 13, 2004 (Table 64; Fig. 97). The two levels of sampling stratification included major habitat types (CHB, UCH, and sand) and fisheries management regimes (open access and MLCD).

Table 64. Sample allocation for south Kohala study area.

Habitat	MLCD	Open	Total
Colonized hardbottom	11	17	28
Uncolonized hardbottom	13	14	27
Sand	10	15	25
Total	34	46	80

Large-scale benthic cover
Benthic coverage for Waialea MLCD derived from the NOAA benthic habitat maps consisted primarily of sand (50%), followed by colonized volcanic rock/boulder (29%), uncolonized volcanic rock/boulder (14%), and aggregated coral (7%) (Table 65).

Table 65. Benthic cover for the Waialea Bay MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized hardbottom	Aggregated coral	9494	6.72
	Colonized volcanic rock/boulder	41410	29.30
Sand		70273	49.73
Uncolonized hardbottom	Uncolonized volcanic rock/boulder	20141	14.25
Grand total		141319	100.00

Small-scale benthic cover of substrate types within the management regimes.
Turf algae was the most abundant substrate type in the MLCD and averaged 42% cover followed by sand with 36% cover (Table 66; Fig. 98). In the open access area, sand cover (38%) was slightly higher than turf algae (36%) cover, but these two substrates were statistically equivalent in the management regimes. Total coral cover was 14% in the MLCD and 19% in the open access area. Ranking of abundant corals was similar in both management regimes with *Porites lobata* (9% - MLCD, 14% - Open) as the most abundant coral followed by *P. compressa* (2% - MLCD, 1% - Open) and *Pocillopora meandrina* (1% - MLCD). Coralline algae cover was similar in the MLCD (5%) compared to outside the reserve (4%). Macroalgae cover averaged 2% in both the MLCD and the open access area, with *Tolypiocladia sp.* (1%) the predominant genus. Macroinvertebrates comprised 1% of the benthic cover with *Echinometra mathaei* (1%) as the most abundant organism in this category.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types (Fig. 98). This result indicated that comparing fish assemblages across the management strata was appropriate at the level of major subtrate types.

<u>Fish assemblage characteristics among habitat types and between management regimes</u>
Fish assemblage characteristics were higher in the MLCD compared with the adjacent open area (Fig. 99, 100, and 101; Table 67A, 67B, and 67C). Biomass appeared higher in the open area near the boundaries of the MLCD but it more likely related to habitat than spillover effect. Richness, biomass, and diversity were all highest in the colonized areas, followed by the uncolonized MLCD habitats (Table 67A, 67B, and 67C; Fig. 102, 103, and 104). Although the colonized open area had comparable assemblage values with the MLCD habitat, the uncolonized habitat had consistently lower values. Very few individuals were observed in the sand, particularly in the open area.

<u>Fish trophic structure between management regimes and among habitats</u>
Herbivores comprised 80% of the biomass in the MLCD and 72% in the open area (Fig. 105). Apex predators accounted for 5% of the biomass in the MLCD and less than 2% in the open area. Over half (55%) of the biomass of apex predators in the MLCD consisted of blue trevally (omilu), with the remainder comprised of the introduced peacock grouper (roi)

<u>Species composition by management regime</u>
The dominant species in the MLCD by IRD was the orangeband surgeonfish (*naenae*), which comprised 25% of the total biomass in that management stratum (Table 68). Other important resource species by weight included the whitebar surgeonfish (*maikoiko*, 9%), orangespine unicornfish (umaumalei, 5%), blue trevally (omilu, 2.6%), and redlip parrotfish (*palukaluka*, 1.8%). In the open area, the top three dominant species by IRD (brown surgeonfish [*maiii*], black durgon [*humuhumuelele*], and saddle wrasse [*hinalea lauwili*]) had little or no resource value (Table 69).

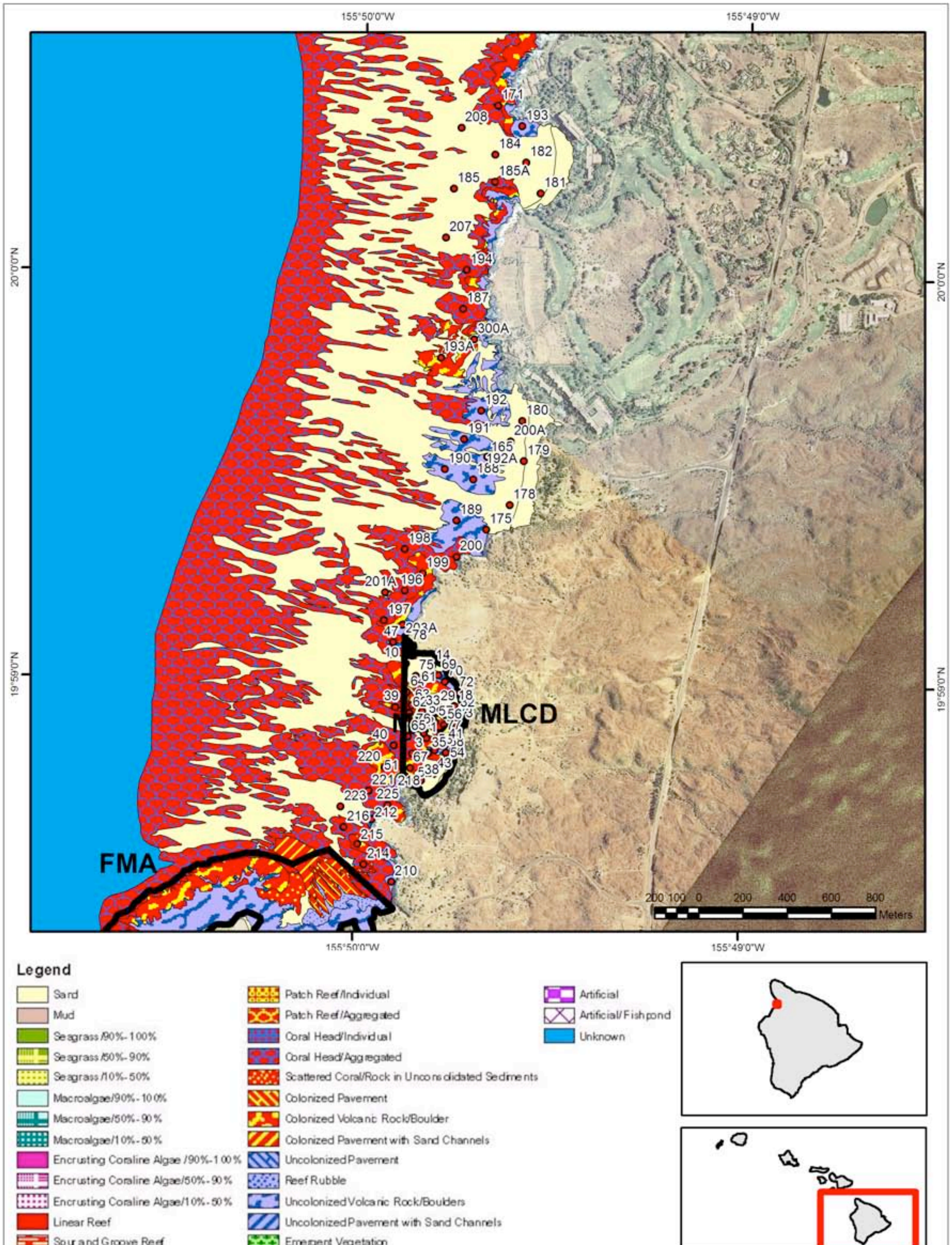

Figure 97. Sampling locations and benthic habitats for the Waialea Bay MLCD and adjacent areas.

Table 66. Top 10 benthic taxa/substrate types by percent cover within the Waialea Marine Life Conservation District (MLCD) and the open access area outside the MLCD.

Marine Life Conservation District			Open Access		
Substrate Type	Taxon	%	Substrate Type	Taxon	%
Turf algae		41.5	Sand		37.8
Sand		35.7	Turf algae		36.2
Coral	*Porites lobata*	9.4	Coral	*Porites lobata*	13.6
Coralline algae		5.2	Coralline algae		4.3
Coral	*Porites compressa*	1.5	Coral	*Porites compressa*	1.4
Macroalgae	*Tolypiocladia sp.*	1.4	Coral	*Pocillopora meandrina*	1.3
Coral	*Pocillopora meandrina*	1.2	Macroalgae	*Tolypiocladia sp.*	1.2
Macroinvertebrate	*Echinometra mathaei*	1.0	Coral	*Montipora capitata*	0.9
Coral	*Porites evermanni*	0.9	Macroinvertebrate	*Echinometra mathaei*	0.7
Macroalgae	*Lyngbya sp.*	0.5	Coral	*Montipora patula*	0.6

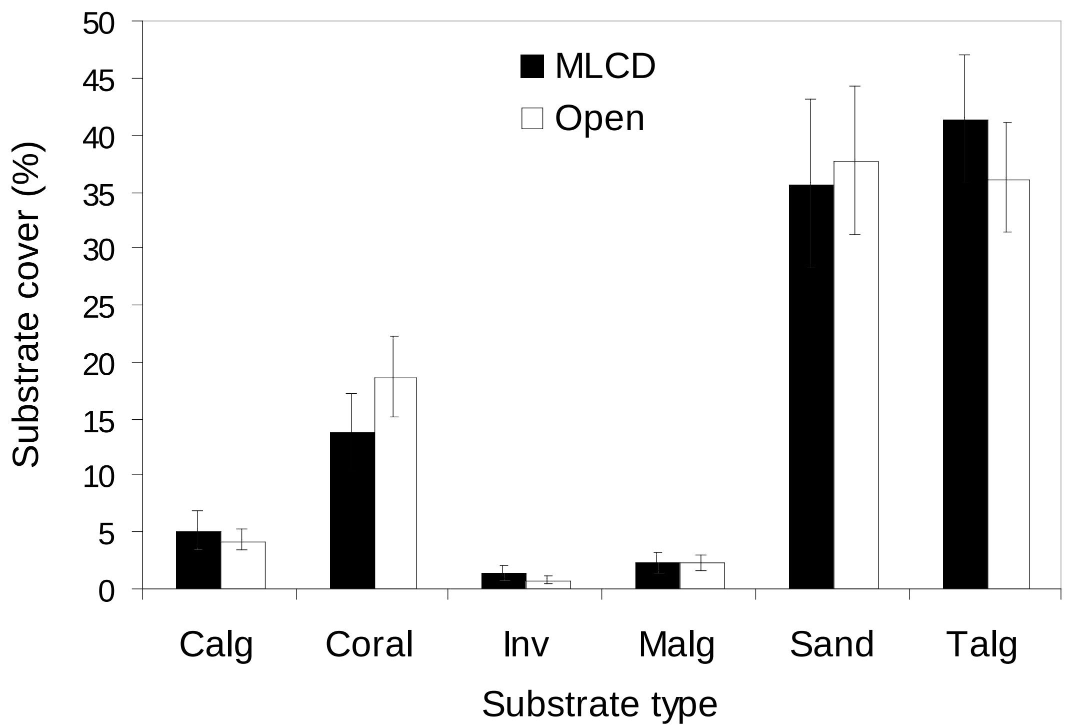

Figure 98. Mean percent cover of substrate types within the Waialea Marine Life Conservation District (MLCD) and outside (Open) of the MLCD. Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

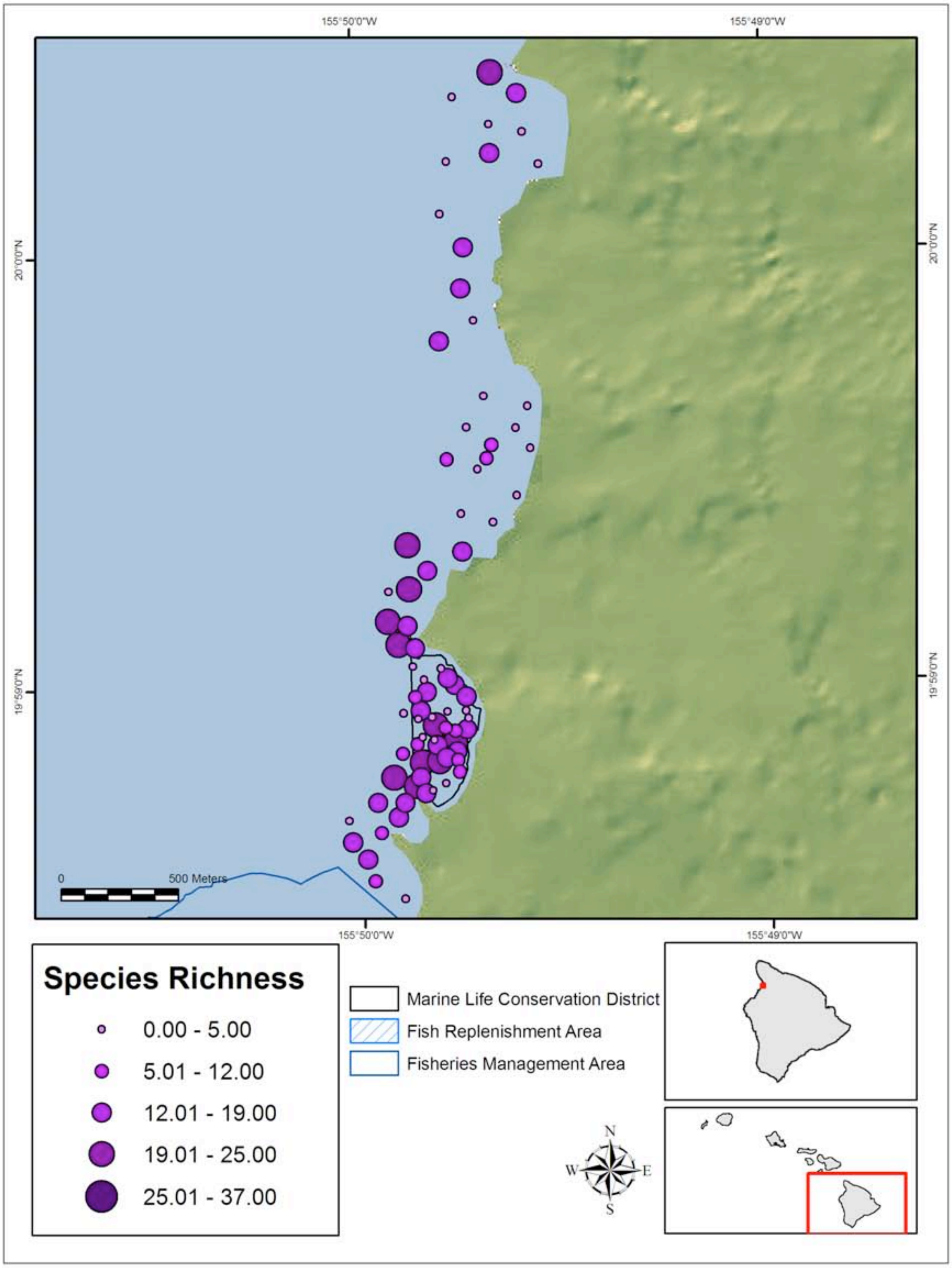

Figure 99. Species richness by individual transects (N=80) for the south Kohala study area, including Waialea Bay MLCD. Classification based on quantiles.

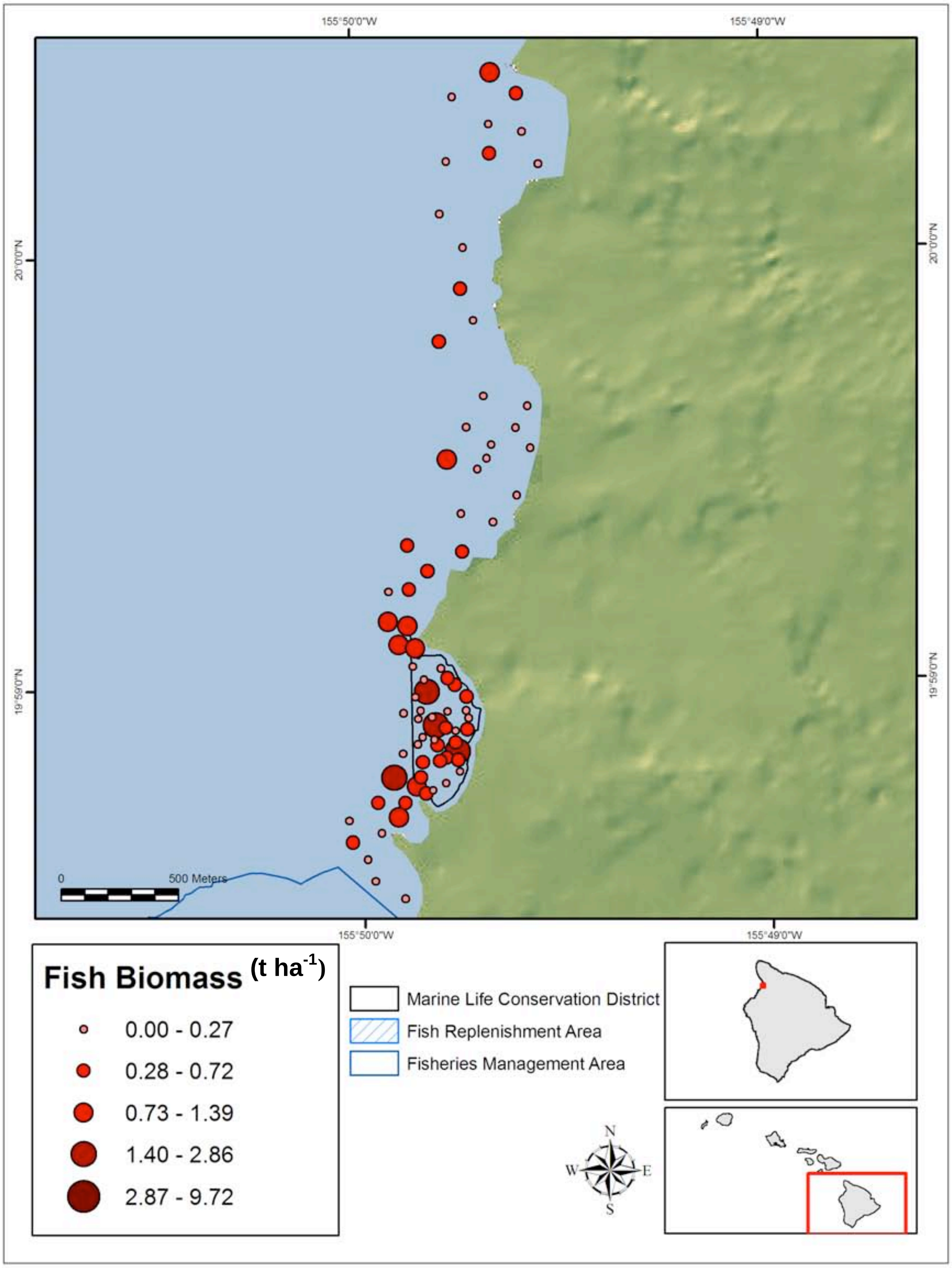

Figure 100. Fish biomass (t ha^{-1}) by individual transects (N=80) for the south Kohala study area, including Waialea Bay MLCD. Classification based on quantiles.

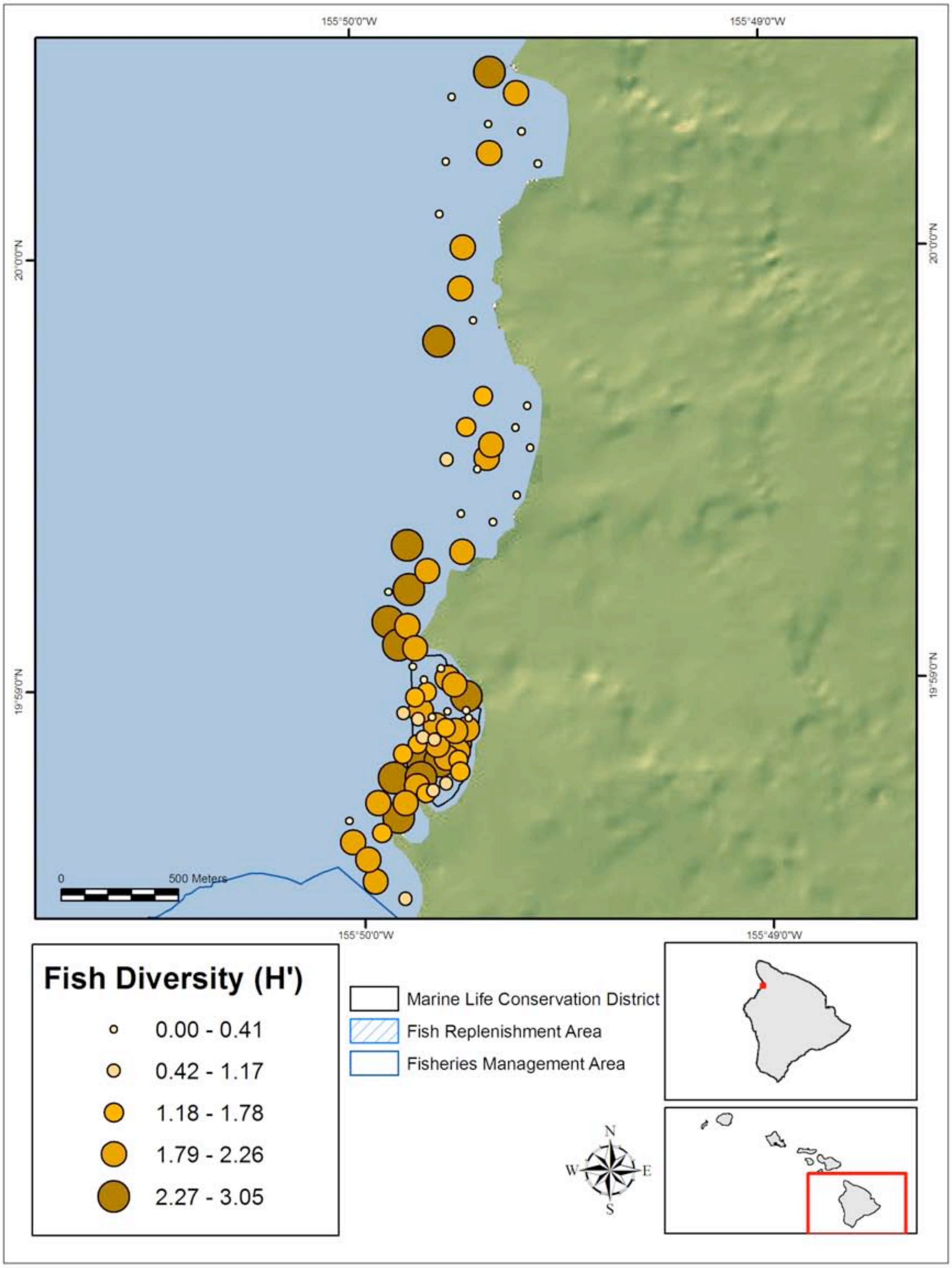

Figure 101. Fish diversity (H') by individual transects (N=80) for the south Kohala study area, including Waialea Bay MLCD. Classification based on quantiles.

Table 67A. Comparison of fish species richness among management regimes and habitat types. Results of nested ANOVA with major habitat types common to all management regimes nested within this management regime (N = 80). Management regimes: MLCD ([M]) and Open (completely open to fishing ([O])). Habitat strata: >10% live coral hard bottom (CHB), <10% live coral hard bottom (UCH); and unconsolidated sediment (UCS). Unplanned multiple comparisons among management strata and $habitat_{[management]}$ tested using Tukey's HSD tests. Underlined means are not significantly different ($\alpha = 0.05$)

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	878.5	56.7	<0.001	
Management	1	626.8	40.5	<0.001	MLCD > Open
$Habitat_{[management]}$	4	933.7	60.3	<0.001	
Error	63	15.5			
$Habitat_{[management]}$ -					$CHB_{[M]}$ $UCH_{[M]}$ $CHB_{[O]}$ $UCH_{[O]}$ $UCS_{[M]}$ $UCS_{[O]}$

Table 67B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	0.83	20.3	<0.0001	
Management	1	1.82	44.4	<0.0001	MLCD > Open
$Habitat_{[management]}$	4	0.56	13.7	<0.0001	
Error	63	0.04			
$Habitat_{[management]}$ -					$CHB_{[M]}$ $UCH_{[M]}$ $CHB_{[O]}$ $UCH_{[O]}$ $UCS_{[M]}$ $UCS_{[O]}$

Table 67C. Comparison of fish species diversity (H') among management regimes and habitat types.

Source	d.f.	MS	F	p	Multiple comparisons
Model	5	10.7	58.8	<0.001	
Management	1	3.8	20.7	<0.001	MLCD > Open
$Habitat_{[management]}$	4	12.6	69.4	<0.001	
Error	63	0.2			
$Habitat_{[management]}$ -					$CHB_{[M]}$ $UCH_{[M]}$ $CHB_{[O]}$ $UCH_{[O]}$ $UCS_{[M]}$ $UCS_{[O]}$

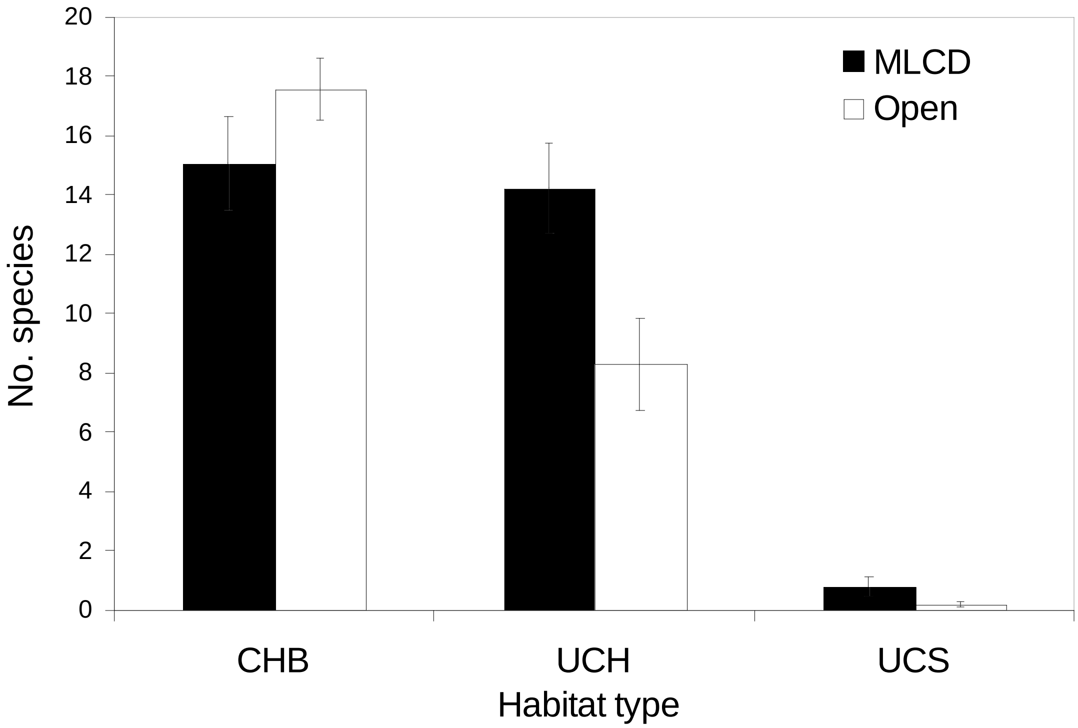

Figure 102. Mean number of species per transect (125 m^2) by habitat type and management regime for the south Kohala study area. Error bars are standard error of the mean.

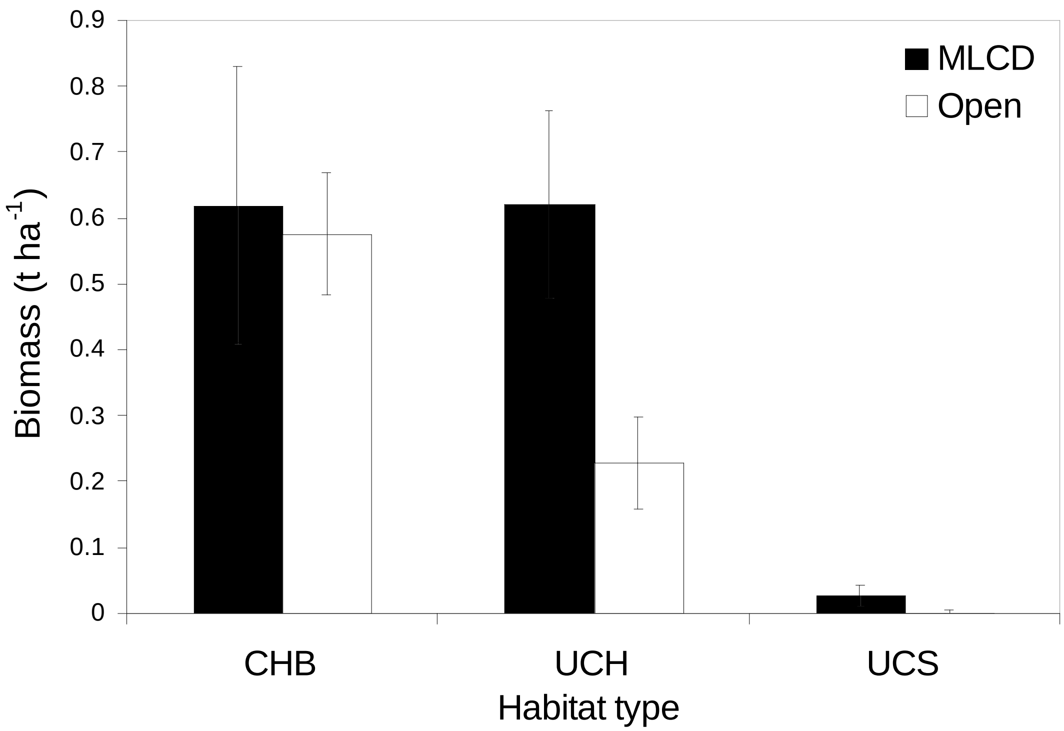

Figure 103. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the south Kohala study area. Error bars are standard error of the mean.

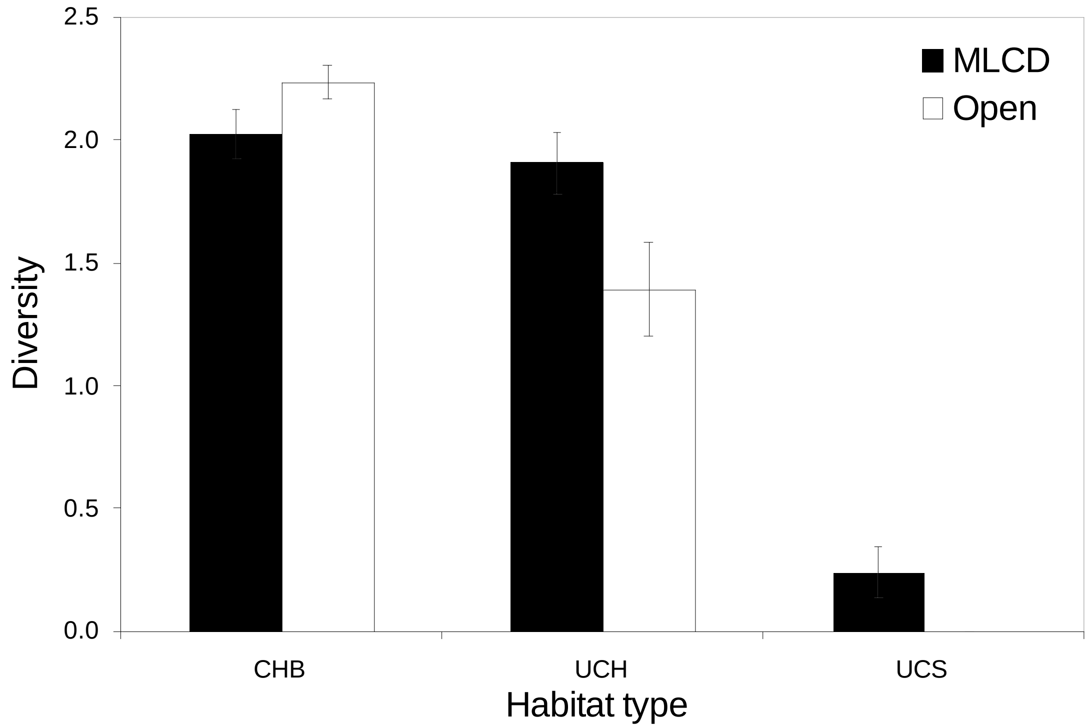

Figure 104. Mean diversity (H’) per transect (125 m^2) by habitat type and management regime for the south Kohala study area. Error bars are standard error of the mean

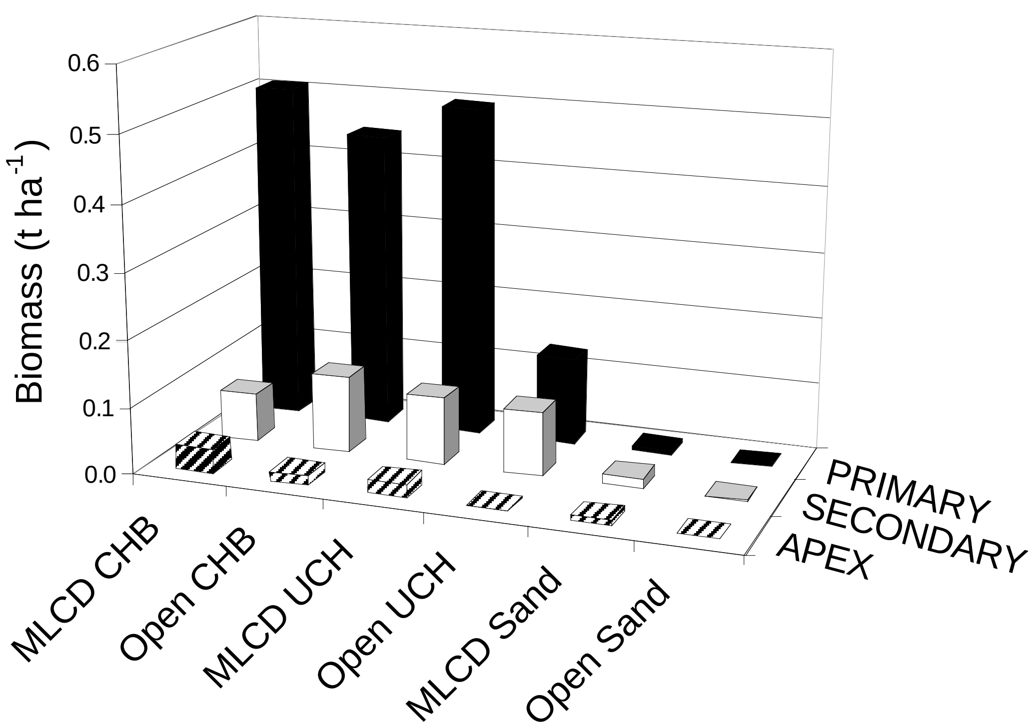

Figure 105. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the south Kohala study area.

Table 68. Top ten species in the Waialea Bay MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.30	0.113	41.18	7.36	25.39	1045.60
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	1.05	0.067	58.82	25.60	14.94	878.69
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.25	0.042	32.35	6.04	9.45	305.84
Melichthys niger	Black Durgon	*humuhumuelele*	0.06	0.043	20.59	1.55	9.67	199.14
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.70	0.010	67.65	17.03	2.27	153.48
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.05	0.022	23.53	1.21	5.03	118.33
Rhinecanthus rectangulus	Reef Triggerfish	*humuhumunukunuk uapuaa*	0.06	0.010	41.18	1.38	2.24	92.41
Abudefduf sordidus	Blackspot Sargent	*kupipi*	0.07	0.013	29.41	1.73	3.02	88.96
Caranx melampygus	Blue Trevally	*omilu*	0.03	0.012	23.53	0.69	2.63	61.90
Scarus rubroviolaceus	Redlip Parrotfish	*palukaluka*	0.06	0.008	32.35	1.38	1.77	57.41

Table 69. Top ten species in the south Kohala open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.82	0.041	56.52	24.50	14.54	822.05
Melichthys niger	Black Durgon	*humuhumuelele*	0.07	0.031	21.74	2.09	10.91	237.23
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.58	0.009	58.70	17.26	3.26	191.30
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.04	0.015	28.26	1.30	5.39	152.42
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.15	0.010	28.26	4.48	3.60	101.74
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.04	0.010	26.09	1.20	3.40	88.76
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.06	0.012	19.57	1.77	4.22	82.55
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.04	0.010	19.57	1.15	3.56	69.60
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.06	0.006	28.26	1.67	2.02	57.09
Scarus rubroviolaceus	Redlip Parrotfish	*palukaluka*	0.06	0.004	32.61	1.88	1.56	50.89

Kealakekua Bay MLCD and south Kona

The south kona study area extended from Nenue Point to Honaunau Bay (11.8km) and included the Kealakekua Bay MLCD.

Sample allocation

A total of 76 samples were collected between October 4 and 18, 2004 (Table 70; Fig. 106A and 106B). The two levels of sampling stratification included major habitat types (CHB, UCH, and sand) and fisheries management regimes (open access and MLCD).

Table 70. Sample allocation for south Kona study area.

Habitat	FMA	MLCD	Open	Total
Colonized hardbottom	29	22	13	64
Sand		12		12
Total	29	34	13	76

Large-scale benthic cover

Benthic coverage for Kealakekua Bay MLCD derived from the NOAA benthic habitat maps consisted primarily of sand (62%), followed by aggregated coral (19%), colonized volcanic rock/boulder (15%), and uncolonized volcanic rock/boulder (4%) (Table 71).

Table 71. Benthic cover for the Kealakekua Bay MLCD derived from NOAA benthic habitat maps.

Habitat type	Habitat modifier	Area (m^2)	Percentage
Colonized hardbottom	Aggregated coral	231948	18.78
	Colonized volcanic rock/boulder	191879	15.53
Sand		767343	62.12
Uncolonized hardbottom	Uncolonized volcanic rock/boulder	44139	3.57
Grand total		1235309	100.00

Small-scale benthic cover of substrate types within the management regimes.

The most abundant substrate type in the MLCD was sand (38%) compared to turf algae in the open access area (55%) and FMA (46%) (Table 72; Fig. 107). In contrast, turf algae cover in the MLCD was almost half (25%) of the other two management regimes and sand was nearly 40 times more prevalent. Total coral cover averaged 29% in the MLCD, 30% in the open access area, and 37% in the FMA. *Porites lobata* (18%), *P. compressa* (6%), and *Pavona varians* (2%) were the primary coral species found in the MLCD. This pattern was roughly similar to the FMA (*P. lobata* – 22%, *P. compressa* – 8%), *Pocillopora meandrina* – 5%, and *Pavona varians* – 1%) but differed substantially from the open access area (*Pocillopora meandrina* – 15%, *P. lobata* – 13%, and *Montipora capitata* – 1%). Coralline algae cover was similar among the management strata with 7% in the MLCD and 11% in both the open access area and FMA. Macroalgae cover was equivalent in the open access area and FMA (2%), but occupied less than 1% of the benthos in the MLCD. Macorinvertebrates were not abundant at this site and covered between 0.5% (MLCD) to 2% (FMA) of the substrate.

Different management regimes had statistically similar levels of percent cover for each of the 6 substrate types except for sand, which was more abundant in the MLCD than in the other two management strata (Table 72; Fig. 107). In addition, turf algae cover in the MLCD was statistically lower than in the open access area and the FMA. Consequently, the MLCD habitats were considered distinct from the open access area and the FMA and factored into the comparisons of the fish assemblages.

Fish assemblage characteristics among habitat types and between management regimes

Only a small area open to fishing (2km) was present north of the MLCD and south of the Red Hill FRA. Except for biomass, no apparent differences were obvious for assemblage characteristics among management regimes (Fig. 108, 109, and 110). Sand habitat greater than one acre was only present in the MLCD, and therefore, colonized hardbottom was the only habitat common to all three management strata. In this habitat, species richness and diversity were not significantly different between the three management regimes (Fig. 111 and 113; Table 73A and 73C). Biomass was significantly higher in the MLCD but did not differ between the open area and the FMAs (Fig. 112, Table 73B). The sand habitat in the MLCD had high biomass but very high variance.

Fish trophic structure between management regimes and among habitats

In the colonized hardbottom habitat, primary consumers accounted for 60% of the fish biomass in the MLCD and 50% in both the FMA and open area (Fig. 114). Apex predator biomass in this habitat ranged from a low of 4% in the open area to slightly more than 5% in the MLCD. High apex predator biomass in the MLCD sand habitat results from the presence of a school of 20 island jacks (*Carangoides orthogrammus*), a 150cm barracuda (*Sphyraena barracuda*), and a single 35cm jobfish (*uku*, *Aprion virescens*).

Species composition by management regime

Goldring surgeonfish (*kole*) was the dominant species in the MLCD and accounted for 10% of total fish biomass (Table 74). This was followed by yellow tang (*lauipala*), black durgon (*humuhumuelele*), and bullethead parrotfish (*uhu*). In the FMA, yellow tang rank first in IRD, followed by goldring surgeonfish, orangespine unicornfish (*umaumalei*), and brown surgeonfish (*maiii*) (Table 75). In the open area, orangespine surgeonfish dominated, followed by goldring surgeonfish, yellow tang, and brown surgeonfish (Table 76).

Table 72. Top 10 benthic taxa/substrate types by percent cover within the Kealakekua Marine Life Conservation District (MLCD), the open access area outside the MLCD, and inside of the adjacent Fisheries Management Area.

Marine Life Conservation District			Open Access			Fisheries Management Area		
Substrate Type	Taxon	%	Substrate Type	Taxon	%	Substrate Type	Taxon	%
Sand/Bare Rock		38.3	Turf algae		55.4	Turf algae		46.4
Turf algae		24.8	Coral	*Pocillopora meandrina*	15.0	Coral	*Porites lobata*	21.8
Coral	*Porites lobata*	17.7	Coral	*Porites lobata*	12.6	Coralline algae		11.4
Coralline algae		6.8	Coralline algae		10.5	Coral	*Porites compressa*	7.9
Coral	*Porites compressa*	5.8	Macroalgae	*Dictyota sp.*	1.4	Coral	*Pocillopora meandrina*	4.6
Coral	*Pavona varians*	2.3	Coral	*Montipora capitata*	1.0	Coral	*Pavona varians*	1.1
Coral	*Porites evermanni*	0.8	Coral	*Montipora patula*	0.6	Coral	*Montipora capitata*	0.9
Coral	*Pocillopora meandrina*	0.8	Macroinvertebrate	*Anthelia edmondsonii*	0.5	Sand/Bare Rock		0.9
Coral	*Montipora capitata*	0.6	Coral	*Porites compressa*	0.4	Macroinvertebrate	*Echinometra mathaei*	0.7
Coral	*Psammocora nierstraszi*	0.6	Coral	*Porites evermanni*	0.4	Coral	*Porites evermanni*	0.6

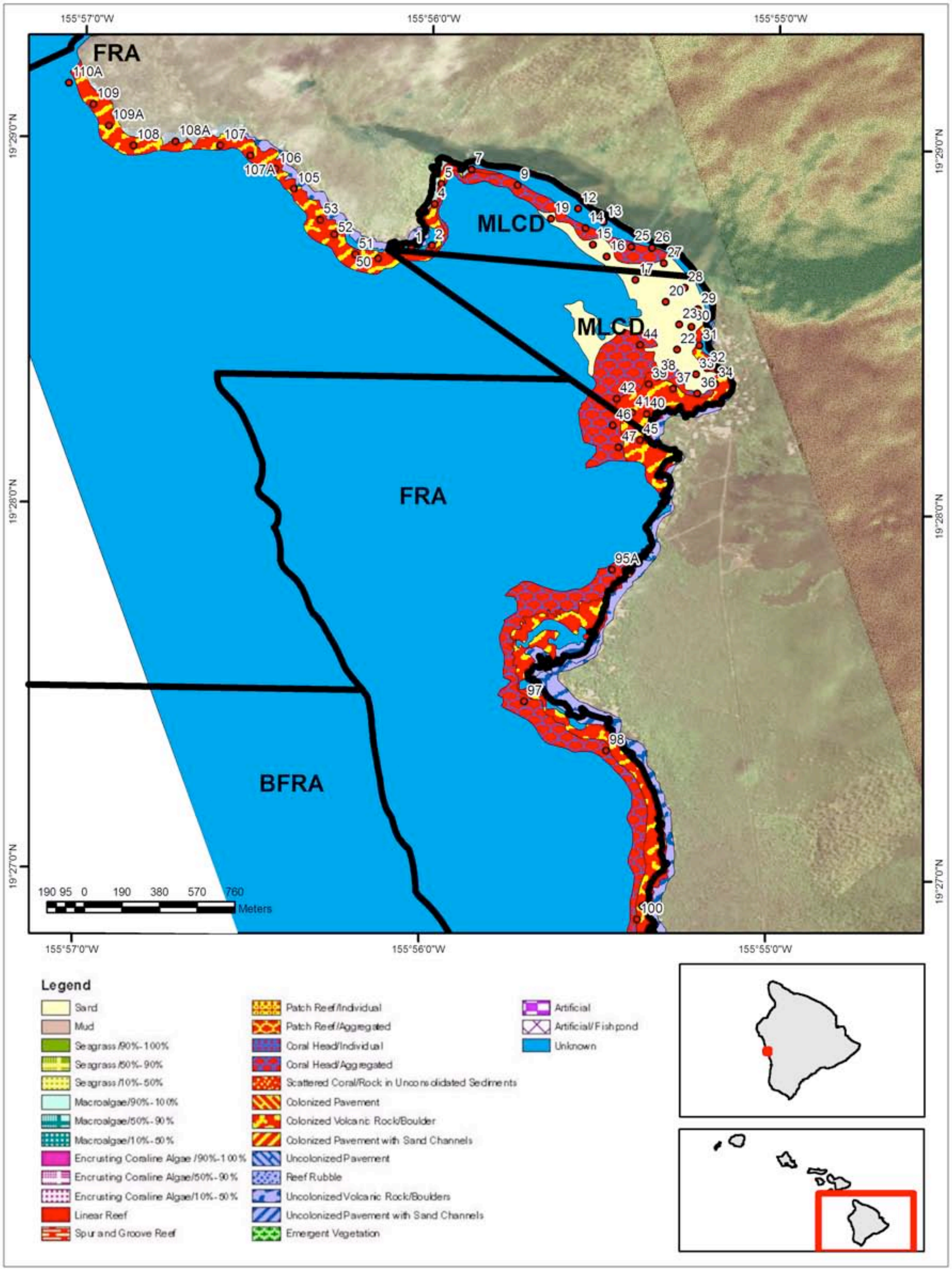

Figure 106A. Sampling locations and benthic habitats for the Kealakekua Bay MLCD and adjacent areas.

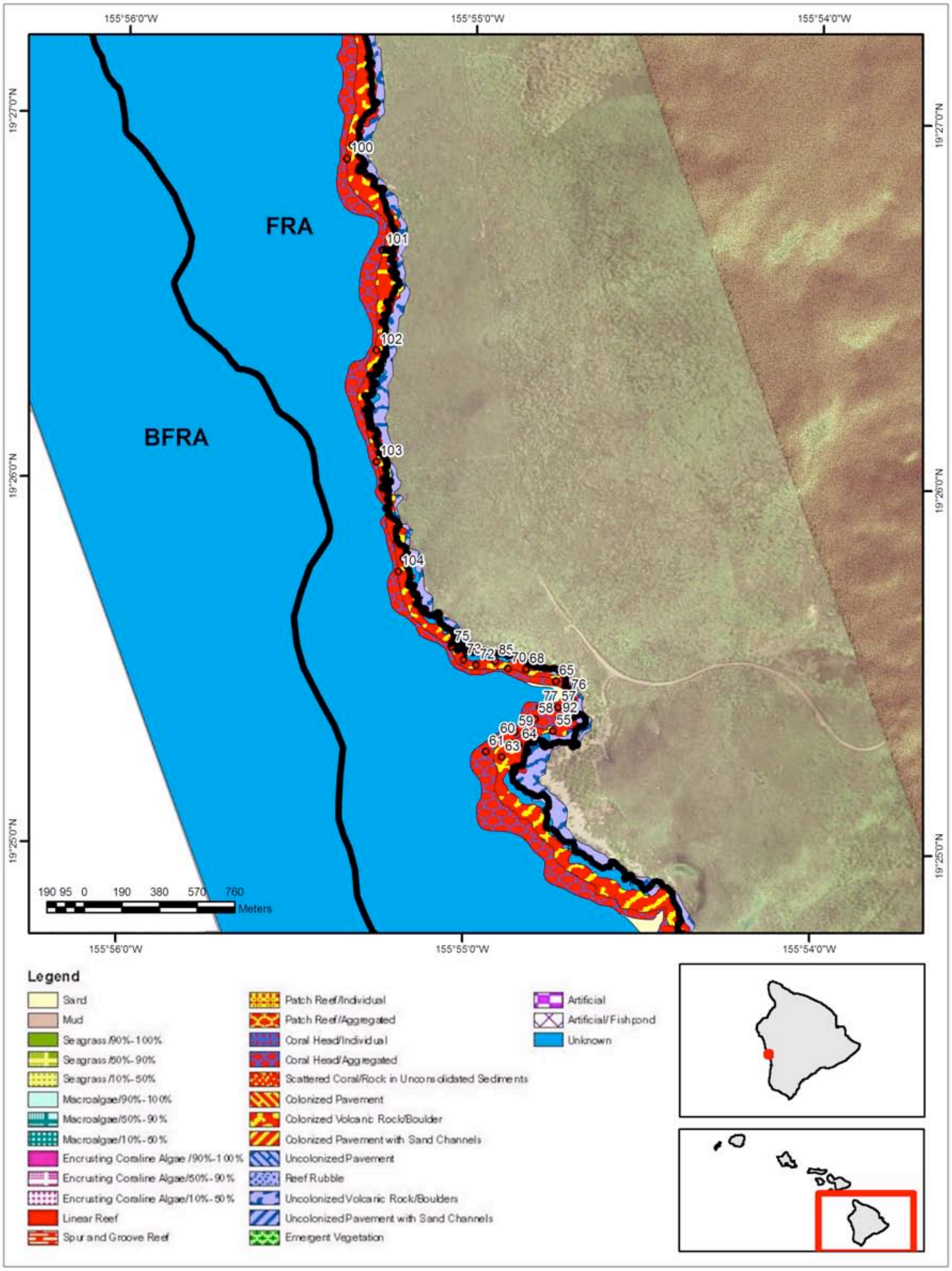

Figure 106B. Sampling locations and benthic habitats for the south Kona study area.

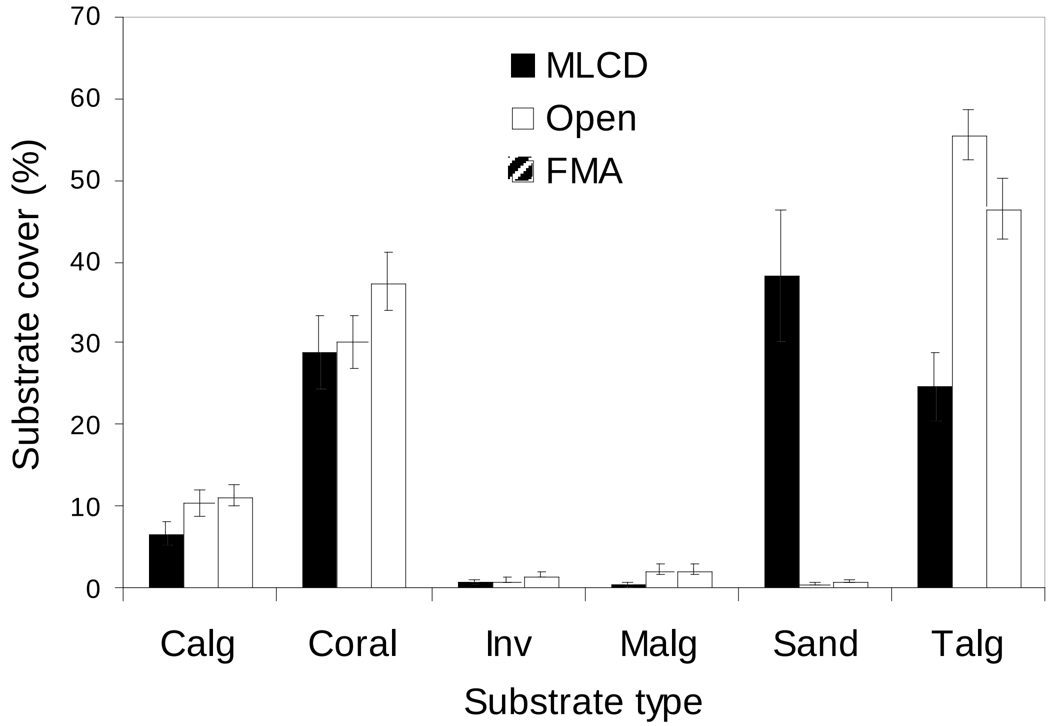

Figure 107. Mean percent cover of substrate types within the Kealakekua Marine Life Conservation District (MLCD), outside (Open) of the MLCD, and inside of the adjacent Fisheries Management Area (FMA). Calg = Coralline algae, Coral = Living coral, Inv = Macroinvertebrates, Malg = Macroalgae, Sand = Sand, Talg = Turf algae. Error bars are ± 1 SE of the mean.

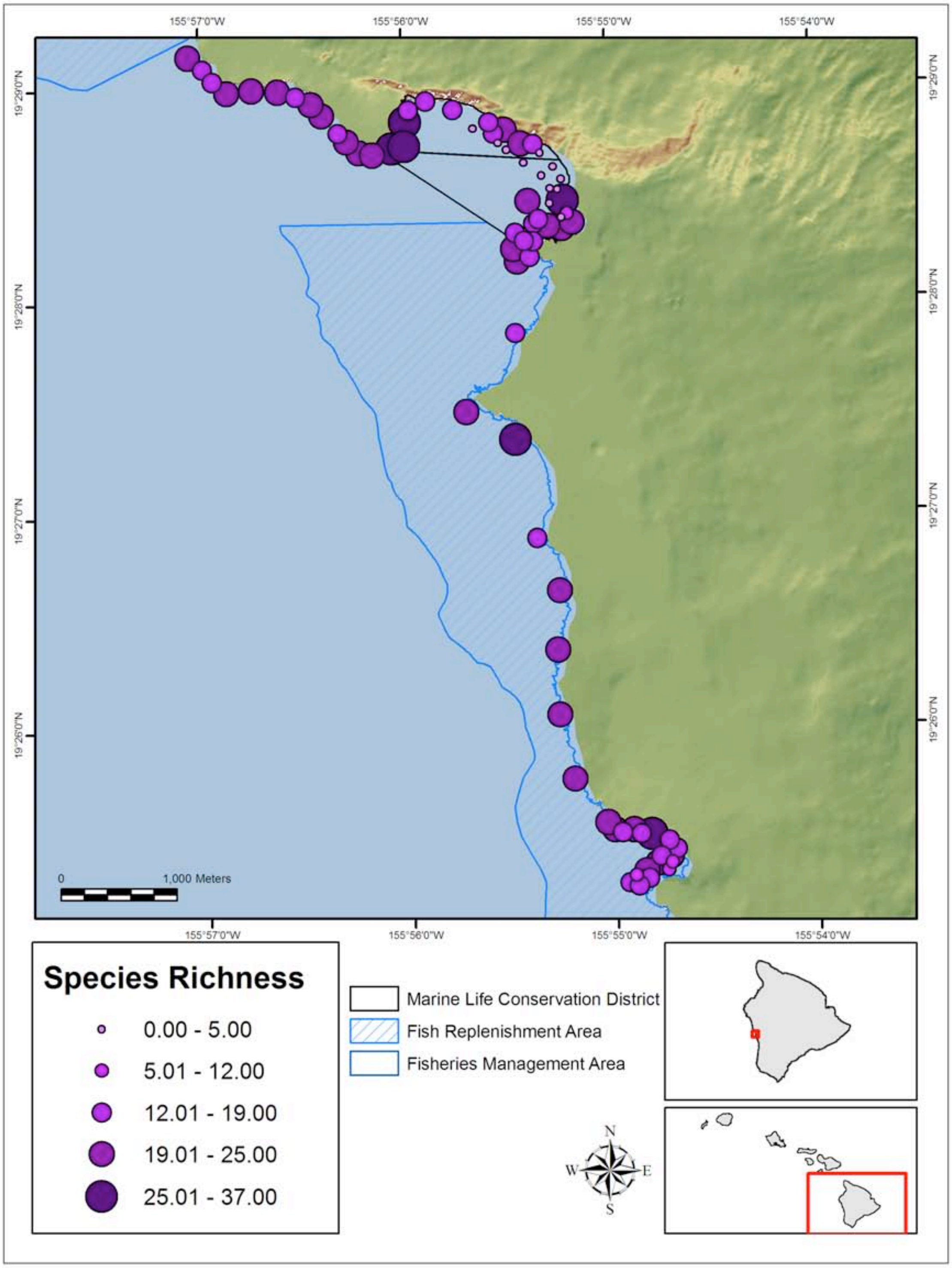

Figure 108. Species richness by individual transects (N=76) for south Kona study area, including Kealakekua Bay MLCD. Classification based on quantiles.

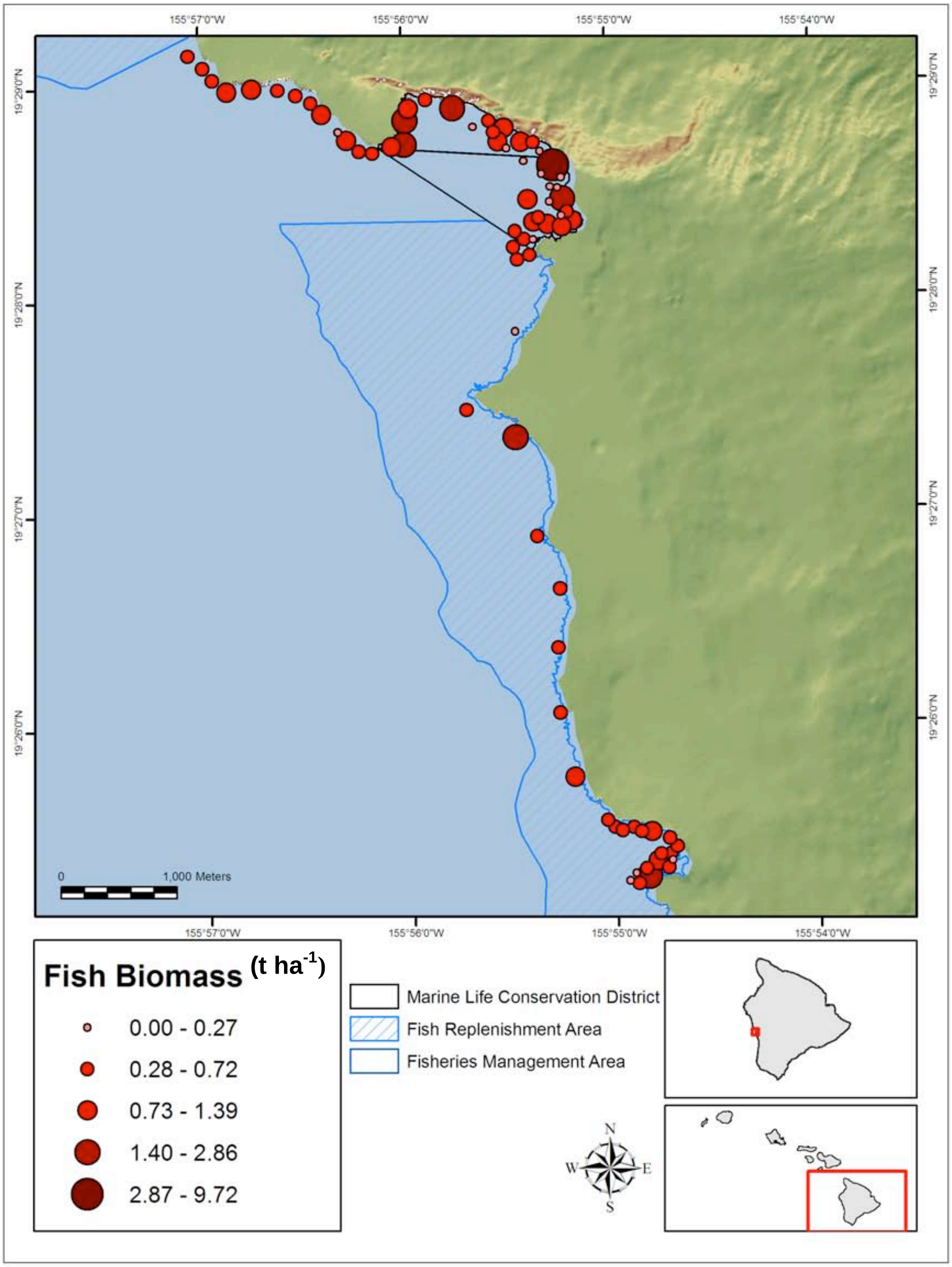

Figure 109. Fish biomass (t ha^{-1}) by individual transects (N=76) for south Kona study area, including Kealakekua Bay MLCD. Classification based on quantiles.

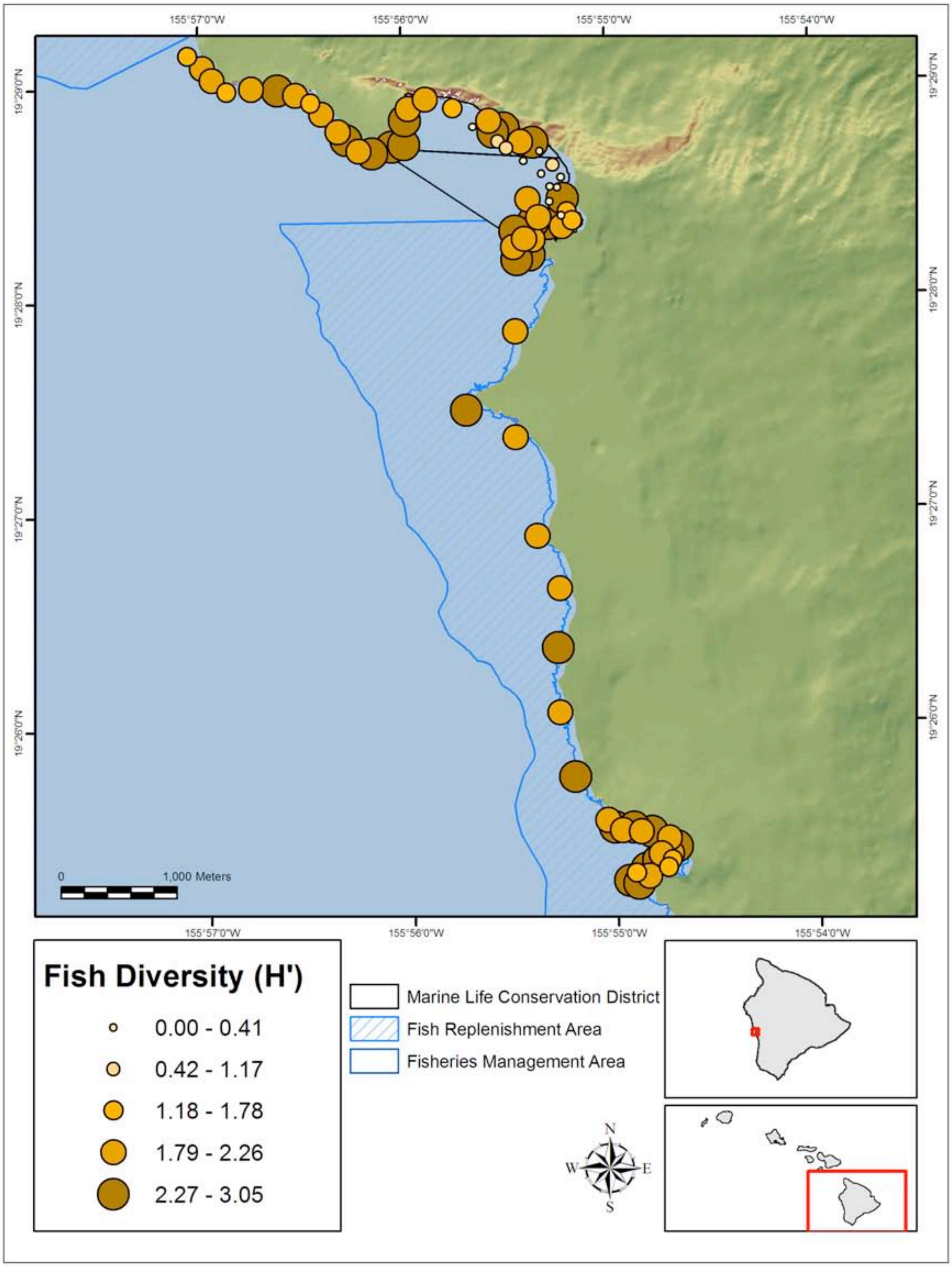

Figure 110. Fish diversity (H') by individual transects (N=76) for south Kona study area, including Kealakekua Bay MLCD. Classification based on quantiles.

Table 73A. Comparison of fish species richness among management regimes and habitat types for the south Kona study area. Results of one-way ANOVA. Colonized hard bottom habitat with >10% live coral (CHB) was the only habitat type common to all management regimes (N = 64). Unplanned multiple comparisons among management strata tested using Tukey's HSD tests. Underlined means are not significantly different (α = 0.05)

Source	d.f.	MS	F	p	Multiple comparisons
Model	2	3.4	0.16	0.85	
Error	61	21.3			
Management -					Open = MLCD = FMA

Table 73B. Comparison of fish biomass (t ha^{-1}) among management regimes and habitat types the south Kona study area. Biomass ln(x+1) transformed prior to analysis.

Source	d.f.	MS	F	p	Multiple comparisons
Model	2	0.17	3.75	0.029	
Error	61	0.04			
Management -					MLCD > Open = FMA

Table 73C. Comparison of fish species diversity (H') among management regimes and habitat types the south Kona study area.

Source	d.f.	MS	F	p	Multiple comparisons
Model	2	0.20	1.73	0.185	
Error	61	0.12			
Management -					FMA = MLCD = Open

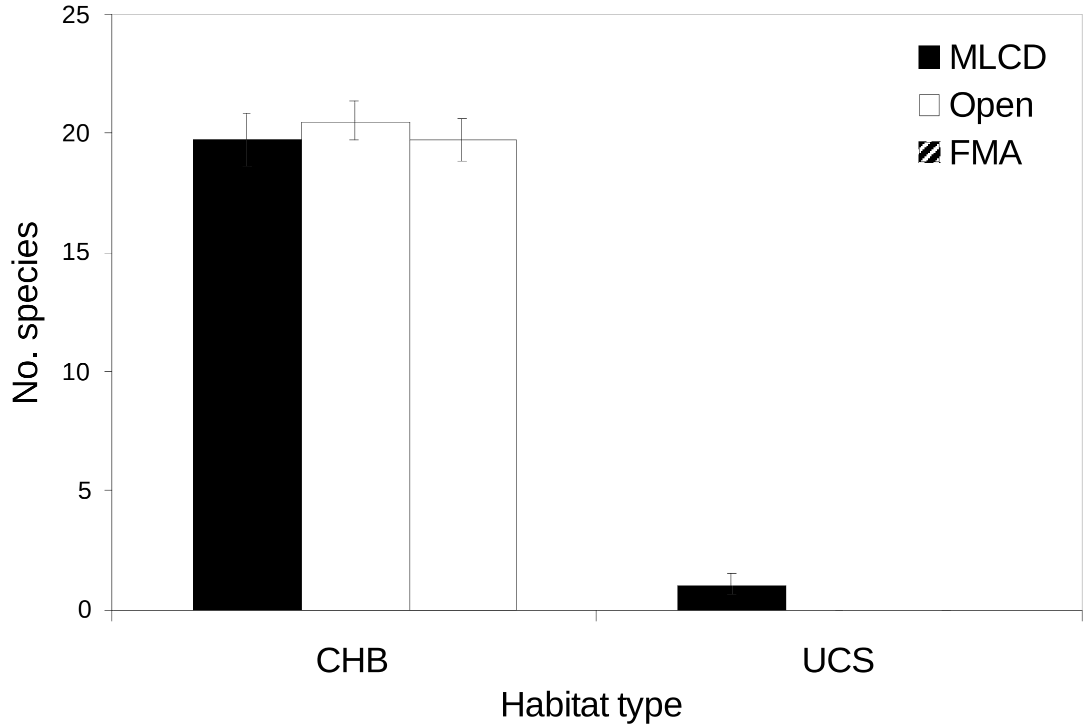

Figure 111. Mean number of species per transect (125 m^2) by habitat type and management regime for the south Kona study area. Error bars are standard error of the mean.

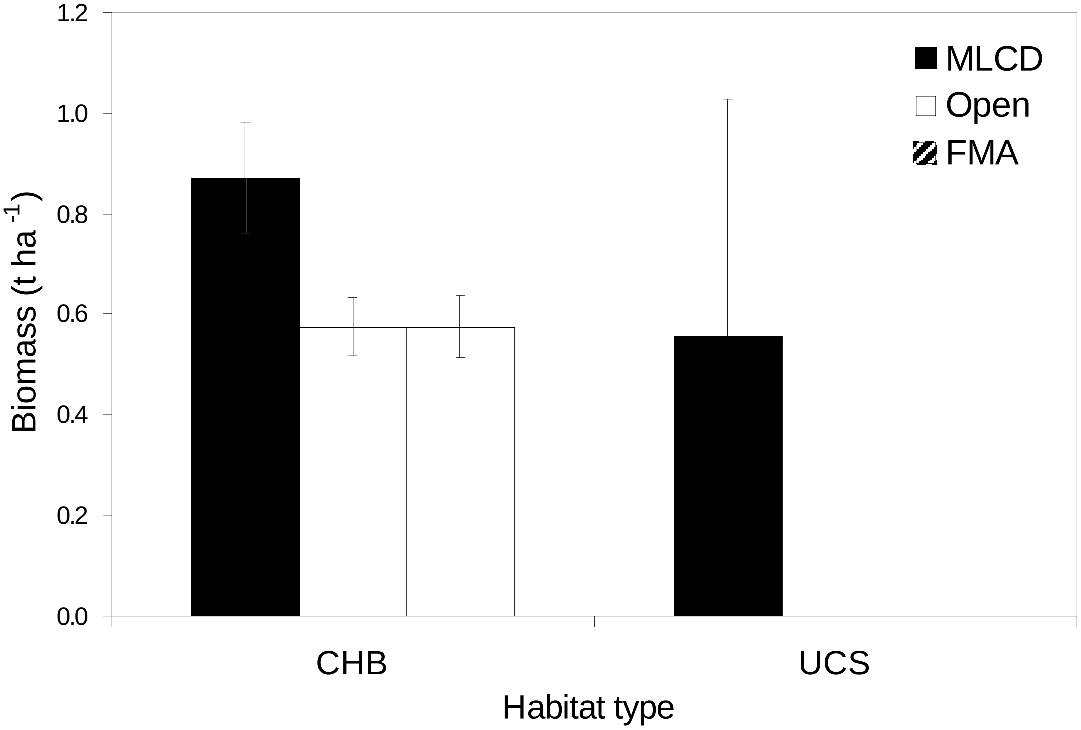

Figure 112. Mean biomass per transect (t ha^{-1}) by habitat type and management regime for the south Kona study area. Error bars are standard error of the mean.

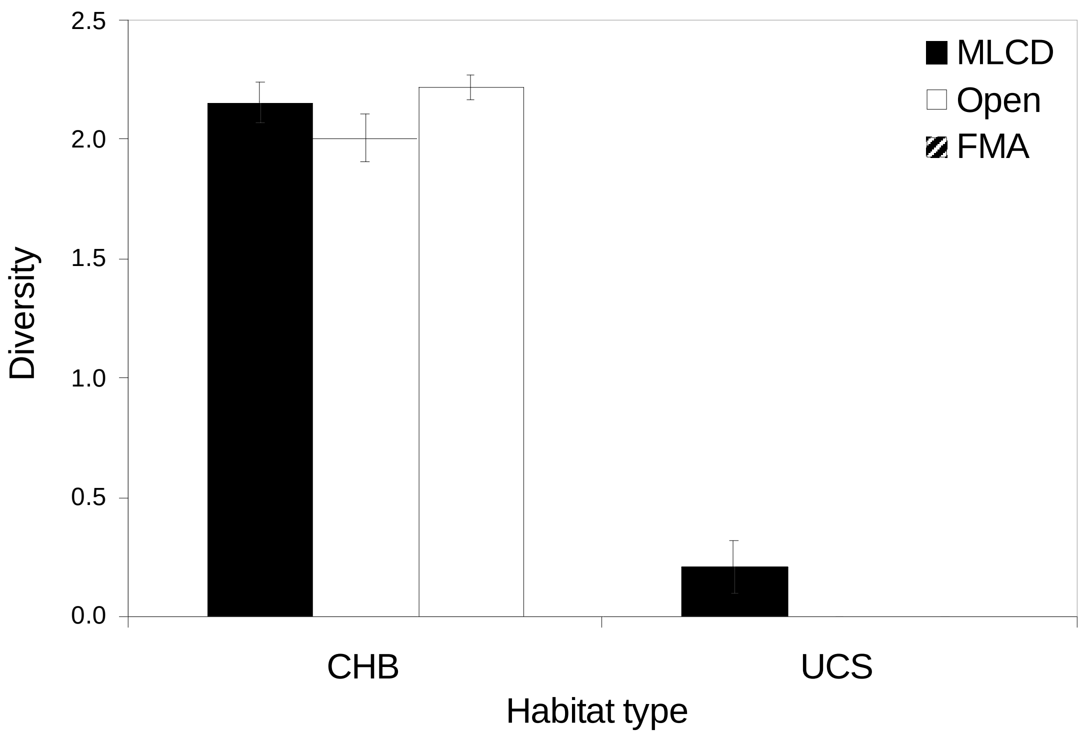

Figure 113. Mean diversity (H') per transect (125 m^2) by habitat type and management regime for the south Kona study area. Error bars are standard error of the mean

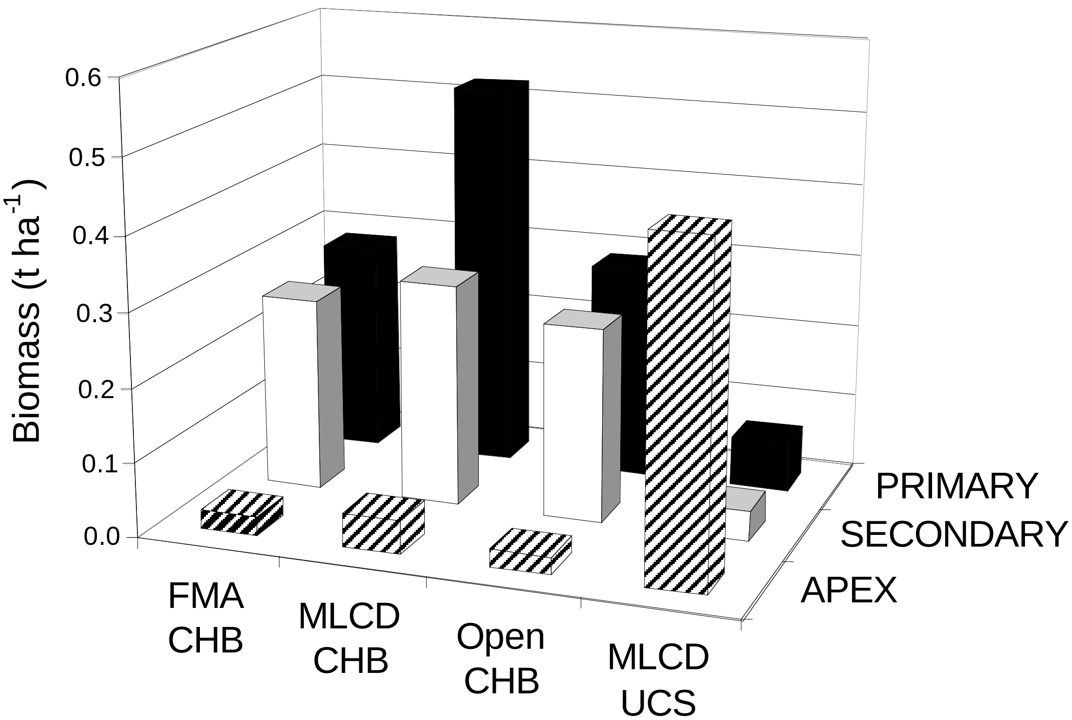

Figure 114. Mean biomass (t ha^{-1}) of major trophic guild by habitat type and management regime for the south Kona study area.

Table 74. Top ten species in the Kealakekua Bay MLCD, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	1.00	0.079	58.82	17.76	10.42	612.68
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.72	0.075	61.76	12.76	9.86	608.93
Melichthys niger	Black Durgon	*humuhumuelele*	0.15	0.079	35.29	2.67	10.37	365.85
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.12	0.068	41.18	2.04	8.88	365.75
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.56	0.021	55.88	9.84	2.71	151.51
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.06	0.025	35.29	1.13	3.32	117.12
Cephalopholis argus	Blue-spotted Grouper		0.06	0.030	29.41	1.04	3.95	116.07
Ctenochaetus hawaiiensis	Black Surgeonfish		0.07	0.026	23.53	1.25	3.41	80.18
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.04	0.018	32.35	0.67	2.34	75.80
Sphyraena barracuda	Barracuda		0.00	0.142	2.94	0.04	18.65	54.85

Table 75. Top ten species in the Napoopoo-Honaunau FRA (FMA), ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Zebrasoma flavescens	Yellow Tang	*lauipala*	1.27	0.105	96.55	14.30	18.25	1761.97
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	1.32	0.079	79.31	14.86	13.83	1096.73
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.13	0.041	68.97	1.43	7.20	496.86
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	0.67	0.023	93.10	7.57	4.05	376.84
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.06	0.023	48.28	0.72	4.07	196.37
Thalassoma duperrey	Saddle Wrasse	*hinalea lauwili*	0.51	0.009	93.10	5.73	1.55	144.30
Acanthurus leucopareius	Whitebar Surgeonfish	*maikoiko*	0.14	0.029	24.14	1.62	5.02	121.12
Cephalopholis argus	Blue-spotted Grouper		0.05	0.016	37.93	0.56	2.83	107.29
Paracirrhites arcatus	Arc-eye Hawkfish	*pili koa*	0.39	0.007	82.76	4.46	1.15	95.09
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.07	0.009	58.62	0.75	1.57	92.22

Table 76. Top ten species in the south Kona open area, ordered by Index of Relative Dominance (IRD = % freq. x % biomass). No. = numerical density in number of individuals per hectare x 1000. Biomass = biomass density in t ha^{-1}. % freq. = percent frequency of occurrence on all transects within the management regime. % no. = percentage of total number of individuals within management regime. % biomass = percentage of total biomass within the management regime.

Taxon name	Common name	Hawaiian name	No. (no. ha^{-1} x 1000)	Biomass (t ha^{-1})	% freq.	% no.	% biomass	IRD
Naso lituratus	Orangespine Unicornfish	*umaumalei*	0.15	0.065	100.00	1.24	11.31	1131.05
Ctenochaetus strigosus	Goldring Surgeonfish	*kole*	0.84	0.072	84.62	6.77	12.49	1056.90
Zebrasoma flavescens	Yellow Tang	*lauipala*	0.51	0.060	100.00	4.13	10.44	1043.63
Acanthurus nigrofuscus	Brown Surgeonfish	*maiii*	1.09	0.046	100.00	8.81	7.90	790.36
Chlorurus sordidus	Bullethead Parrotfish	*uhu*	0.10	0.061	53.85	0.85	10.51	565.79
Chromis vanderbilti	Blackfin Chromis		5.82	0.018	92.31	47.01	3.09	284.92
Paracirrhites arcatus	Arc-eye Hawkfish	*pili koa*	0.78	0.017	92.31	6.32	3.02	278.99
Chaetodon multicinctus	Multiband Butterflyfish	*kikakapu*	0.34	0.014	92.31	2.74	2.45	226.36
Acanthurus olivaceus	Orangeband Surgeonfish	*naenae*	0.07	0.021	61.54	0.60	3.62	222.95
Sufflamen bursa	Lei Triggerfish	*humuhumulei*	0.08	0.013	76.92	0.65	2.19	168.16

Overall comparisons

<u>Overall habitat comparisons</u>

The most abundant substrate type among all of the study sites and management regimes was turf algae, which averaged 48% cover (Table 77). It ranged from a low of 13% at the Marine Laboratory Refuge in Kaneohe Bay to 72% in the open access areas around the Old Kona Airport. Sand averaged 23% cover overall and was prevalent at most of the sites except for Waikiki FMA, Lapakahi, WaiOpae, Kealakekua FMA and open access sites, and Old Kona Airport MLCD and open access sites. Coral cover averaged 16% and ranged from 1-2% in Waikiki to 38% in the FMA adjacent to Kealakekua Bay. In general, average coral cover was higher on the big island (22%) and Maui (17%) sites compared to the Oahu (9%) sites. Macroalgae averaged 7% overall, and was most abundant in the Waikiki FMA (25%) compared to the Old Kona Airport MLCD (<1%). In fact, four of the top five macroalgae sites (Waikiki FMA, Kaneohe Bay open access and MLCD, and Hanauma Bay open access) were on Oahu. Coralline algae averaged 5% cover among all of the sites, with higher average coverage on the big island (8%) compared to Maui with only 2% average cover. Macroinvertebrate cover averaged 1% with the highest abundance found at the Old Kona Airport MLCD (5%) and other big island sites. Few (<1%) macroinvertebrates were observed at the Oahu sites and Honolua MLCD. It should be noted, however, that the sampling design (e.g. diurnal) did not target this portion of the assemblage. Seagrasses were not abundant, but were documented in the open access areas within Kaneohe Bay (0.3%) and outside of Hanauma Bay (0.1%).

For the focal benthic taxa, coral cover generally was higher than macroalgae cover, but this pattern varied by island, study site, and management regime. At the island level, the Oahu sites had statistically lower coral cover and higher macroalgal cover than the Hawaii, Lanai, and Maui sites (Fig. 115). The one exception was macroalgal cover on Oahu, which was equivalent to the Maui sites. The atypical pattern documented on Oahu was attributed primarily to Waikiki, Pupukea, and Hanauma Bay, although macroalgal cover among all of the study sites was highest in Kaneohe Bay (Fig. 116). Coral cover was also statistically higher in the MLCDs compared to the open access areas with FMAs in between (Fig. 117). In contrast, macroalgae cover was lowest in the MLCDs and highest in the open access areas.

Comparisons among the colonized hardbottom communities across all of the study sites and management regimes revealed 3 distinctive assemblages (Fig. 118). Group A included only the open access area around Waikiki which were characterized by low coral cover, high turf algae, and high macroalgal cover. Group B comprised the bulk of study sites with similar levels of coral cover and turf algae. Group C was composed of the benthic assemblages in the Kaneohe Bay open access areas and marine laboratory refuge. As documented in previous studies (Friedlander et al. 2003), this bay has a unique assemblage not found anywhere else in the state. Two abundant coral species (*Montipora capitata* and *Porites compressa*) coupled with high levels of macroalgal cover (e.g. *Dictyosphaeria sp.* and *Kappaphycus sp.*) resulted in this distinctive grouping.

The uncolonized hardbottom communites also separated into 3 groupings. Group A included Honolua Bay (MLCD and open), Kaneohe Bay (open), Pupukea (open), and Hanauma Bay (open) (Fig. 119). These sites were characterized by a high proportion of macroalgae (e.g.

Acanthophora sp., Dictyosphaeria sp., Galaxura sp., Halimeda sp., and *Microdictyon sp.*) compared to the other study sites. Group B was represented by the hardbottom communites in the WaiOpae MLCD and the open access area. The benthic samples contained a high percentage of cyanobacteria (e.g. *Schizothrix sp.*) and the algae *Ralfsia sp.* Group C comprised the remainder of the study sites with low coral cover and similar levels of coralline algae and macroalgae. Macroalgal taxa appeared to account for the distinctive benthic assemblages in both the colonized and uncolonized hardbottom communities.

Table 77. Average percent cover of substrate types among all of the study sites. Management codes: MLCD = Marine Life Conservation District, MLR = Marine Laboratory Refuge (Moku o Loe), Open = Open Access, FMA = Fisheries Management Area. Substrate type codes: Calg = Coralline algae, Coral = Living Coral, Inv = Macroinvertebrates, Malg = Macroalgae, Plant = Seagrass, Sand = Sand, Talg = Turf algae.

Island	Study Site	Management	Calg	Coral	Inv	Malg	Plant	Sand	Talg
Oahu	Waikiki	FMA	0.0	1.0	0.1	25.2	0.0	4.6	69.1
		MLCD	0.0	1.0	0.0	10.6	0.0	21.2	67.2
		Open	0.2	2.0	0.1	7.9	0.0	24.7	65.1
	Hanauma	MLCD	7.6	14.5	0.9	1.6	0.0	36.5	38.9
		Open	5.6	4.7	0.7	16.7	0.1	30.2	42.0
	Pupukea	MLCD	10.3	6.2	0.0	1.6	0.0	37.6	44.3
		Open	3.7	3.3	0.1	6.4	0.0	33.7	52.8
	Kaneohe Bay	MLR	4.7	32.2	1.2	17.2	0.0	31.8	12.9
		Open	4.9	17.5	0.0	21.9	0.3	32.2	23.3
Maui	Honolua	MLCD	3.5	11.7	0.0	8.9	0.0	35.0	40.8
		Open	1.8	7.6	0.3	12.6	0.0	39.6	38.2
	Molokini	MLCD	1.2	28.5	0.6	0.5	0.0	28.7	40.6
		Open	0.8	21.8	0.2	7.6	0.0	43.8	25.9
Lanai	Manele-Hulopoe	MLCD	4.5	20.0	0.2	0.5	0.0	33.1	41.7
		Open	5.1	12.9	0.1	1.0	0.0	33.3	47.6
Hawaii	Old Kona Airport	FMA	3.6	13.8	3.8	0.7	0.0	32.1	45.9
		MLCD	5.0	24.3	5.3	0.0	0.0	0.5	64.8
		Open	4.2	21.5	1.4	0.1	0.0	0.7	72.1
	Lapakahi	MLCD	10.2	17.1	1.8	0.5	0.0	1.3	69.2
		Open	14.4	21.3	2.4	0.4	0.0	2.2	59.3
	WaiOpae	MLCD	5.9	16.7	0.7	18.3	0.0	2.1	56.3
		Open	9.8	14.5	0.6	14.8	0.0	0.4	59.9
	Waialea	MLCD	5.2	13.8	1.4	2.3	0.0	35.7	41.5
		Open	4.3	18.6	0.8	2.2	0.0	37.8	36.2
	Kealakekua	FMA	11.4	37.5	1.6	2.2	0.0	0.9	46.4
		MLCD	6.8	29.0	0.7	0.4	0.0	38.3	24.8
		Open	10.5	30.3	1.0	2.3	0.0	0.4	55.4

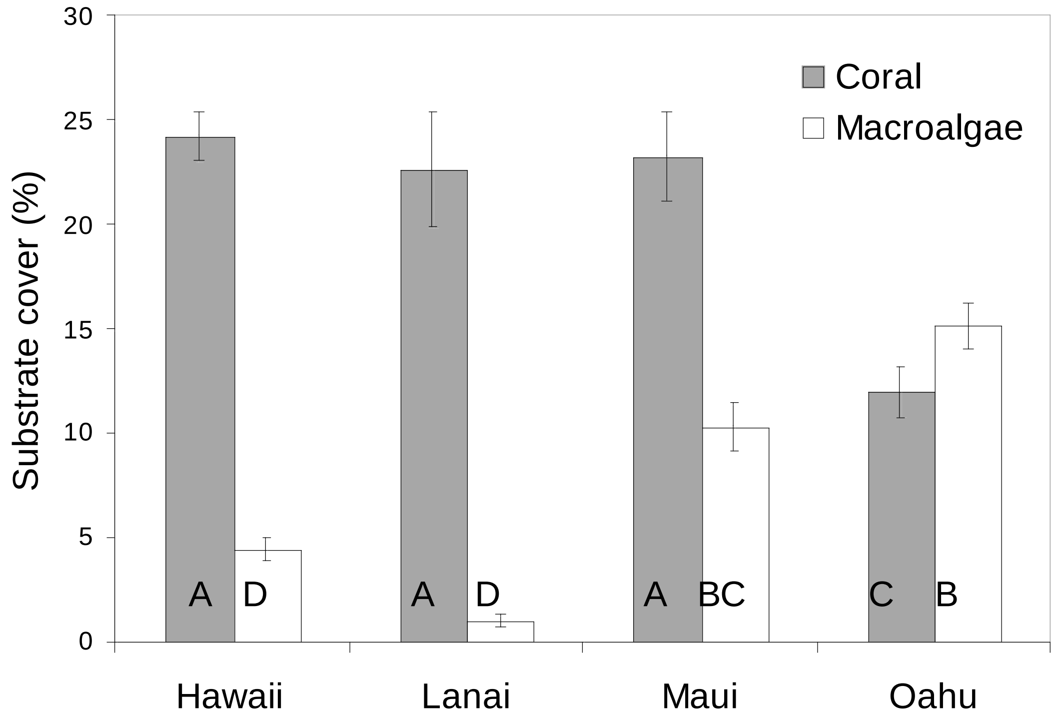

Figure 115. Average percent coral and macroalgae cover by island. Mean cover types with the same letter are not significantly different using a Tukey HSD post-hoc test at α=0.05. Mean ± 1SE. $F_{3,1490} = 63.9$, $p < 0.001$.

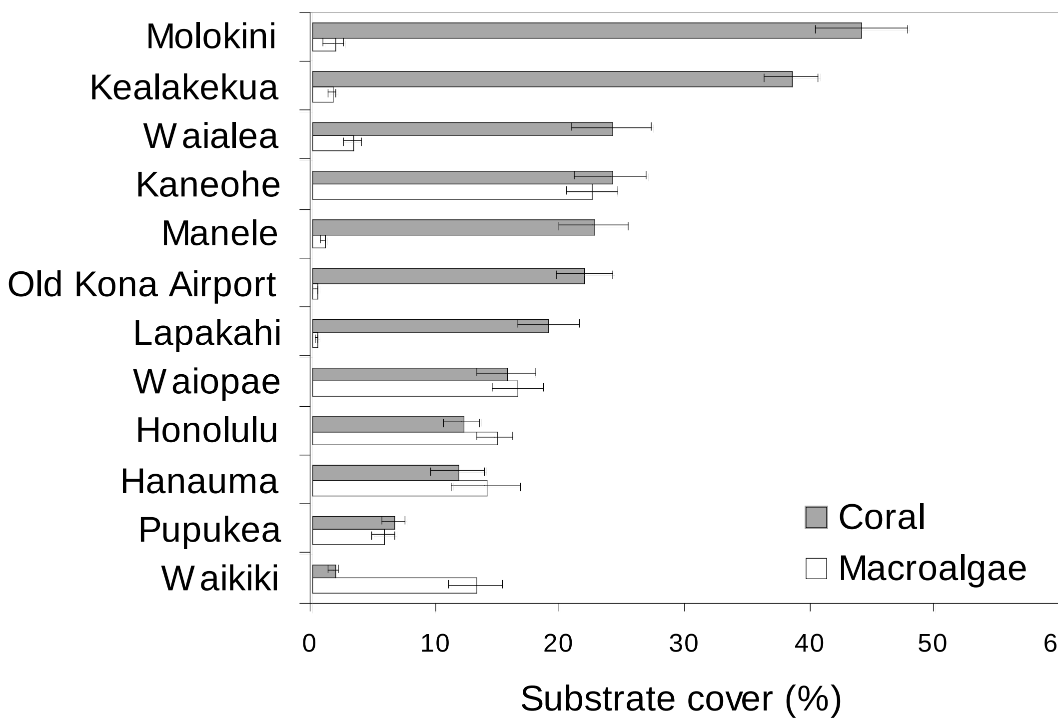

Figure 116. Average percent coral and macroalgae cover by study site. For simplicity and clarity, no multiple comparisons were illustrated on the chart. Mean ± 1SE. $F_{10,\ 1476} = 42.3$, $p < 0.001$.

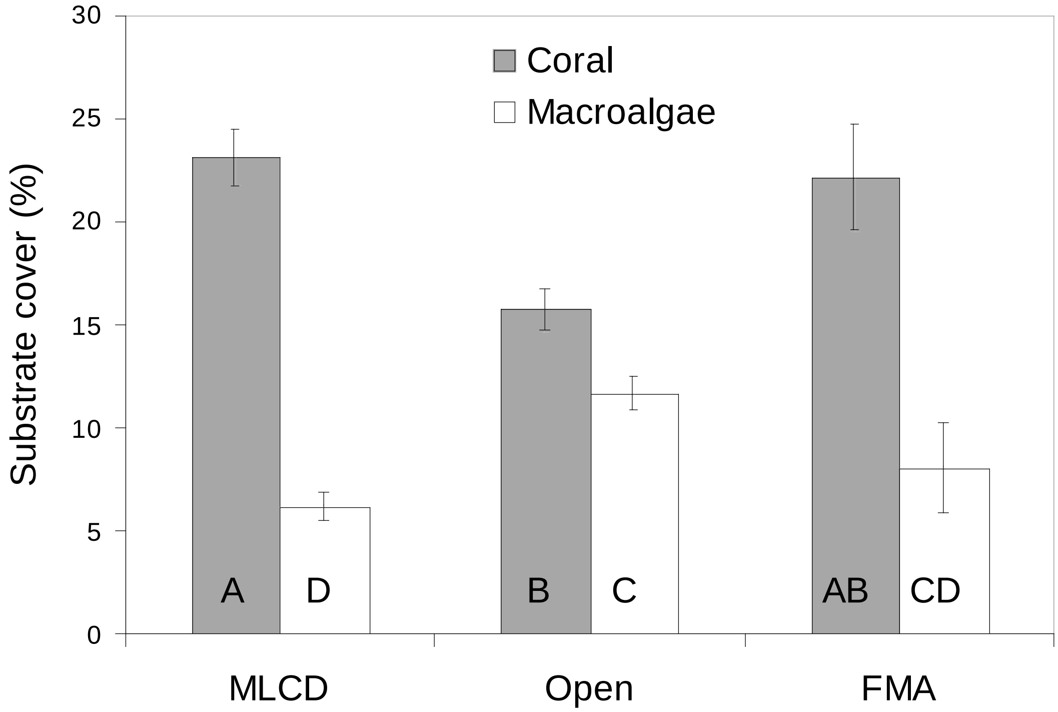

Figure 117. Average percent coral and macroalgae cover by management regime. Substrates in management regimes with the same letter are not significantly different using Tukey HSD post-hoc test at α=0.05. MLCD = Marine Life Conservation District, Open = Open Access, FMA = Fisheries Management Area. Mean ± 1SE. $F_{2, 1492} = 26.89$, $p < 0.001$.

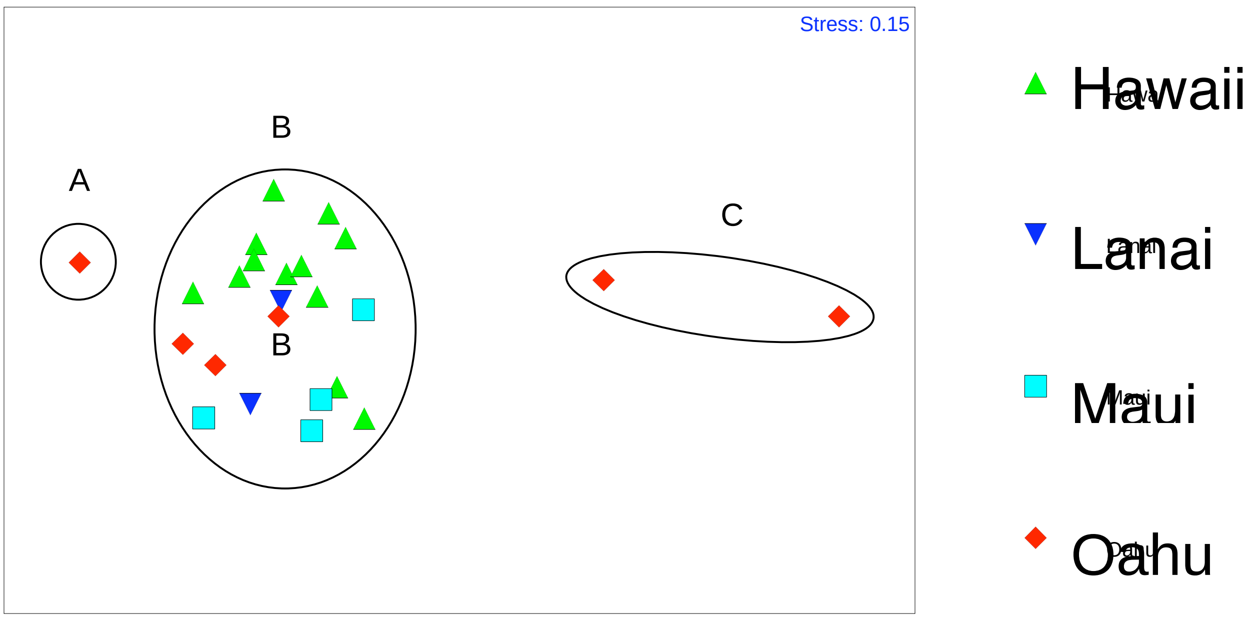

Figure 118. Multidimensional Scaling (MDS) plot of average percent benthic cover on Colonized Hard Bottom (CHB) both inside and outside of the marine protected areas among the different islands. Stress = 0.15. The three distinct groupings (A, B, C) represent unique benthic assemblages.

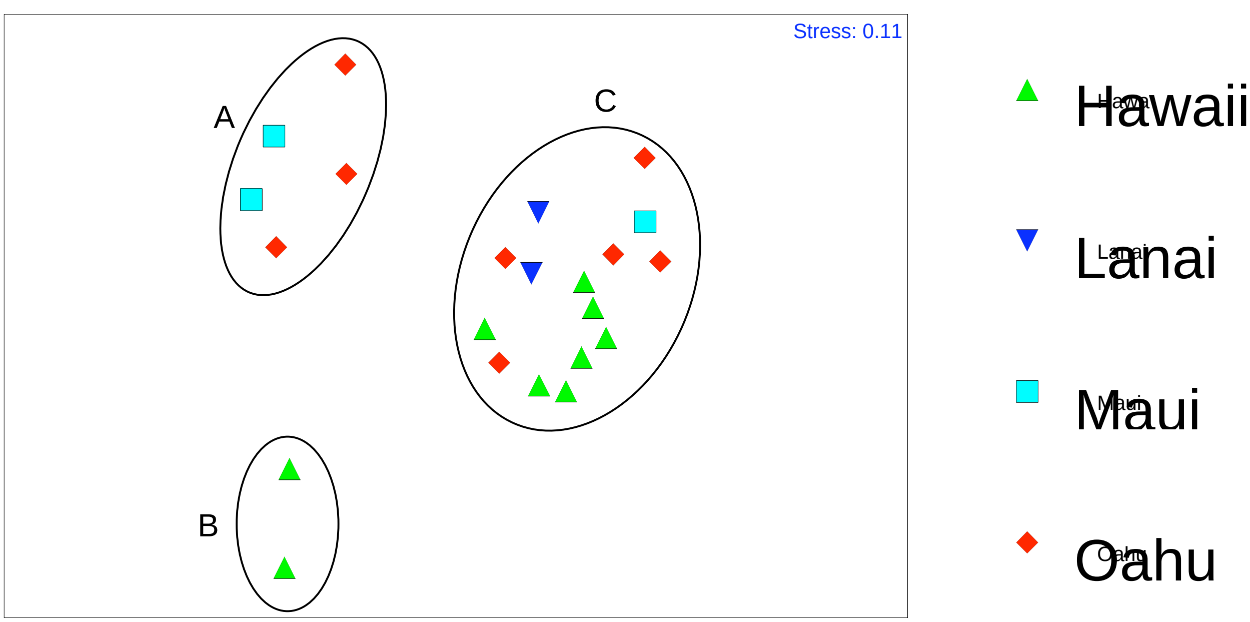

Figure 119. Multidimensional Scaling (MDS) plot of average percent benthic cover on Uncolonized Hard Bottom (UCH) both inside and outside of the marine protected areas among the different islands. Stress = 0.11. The three distinct groupings (A, B, C) represent unique benthic assemblages.

Multivariate comparison of fish assemblages among habitats

Comparison of fish assemblages among all locations showed strong correlations with habitat (Fig. 120). Analysis of Similarities (ANOSIM) among habitat types found significant differences among all habitat types (ANOSIM Global R = 0.51, p <0.001). Pairwise comparisons among habitat types found fish assemblages in the colonized and uncolonized hardbottom habitats to be most similar among all comparisons (Table 78). Much of the macroalgae habitat sampled was macroalgae growing on hard substrate, and as a result showed similarities with the other hardbottom assemblages. The fish assemblages in the sand habitats were highly variable but distinct from the other habitat types.

Table 78. Similarities of fish assemblages among habitat types. Analysis of Similarities (ANOSIM) Global R = 0.51, p <0.001. Pairwise tests results. CHB = colonized hardbottom, UCH = uncolonized hardbottom, MAC = macroalgae, and UCS = unconsolidated sediments (sand).

Habitat comparisons	R statistic	Significance level
CHB & UCH	0.129	0.003
CHB & UCS	0.769	0.001
CHB & MAC	0.846	0.001
UCH & UCS	0.745	0.001
UCH & MAC	0.595	0.001
UCS & MAC	0.440	0.001

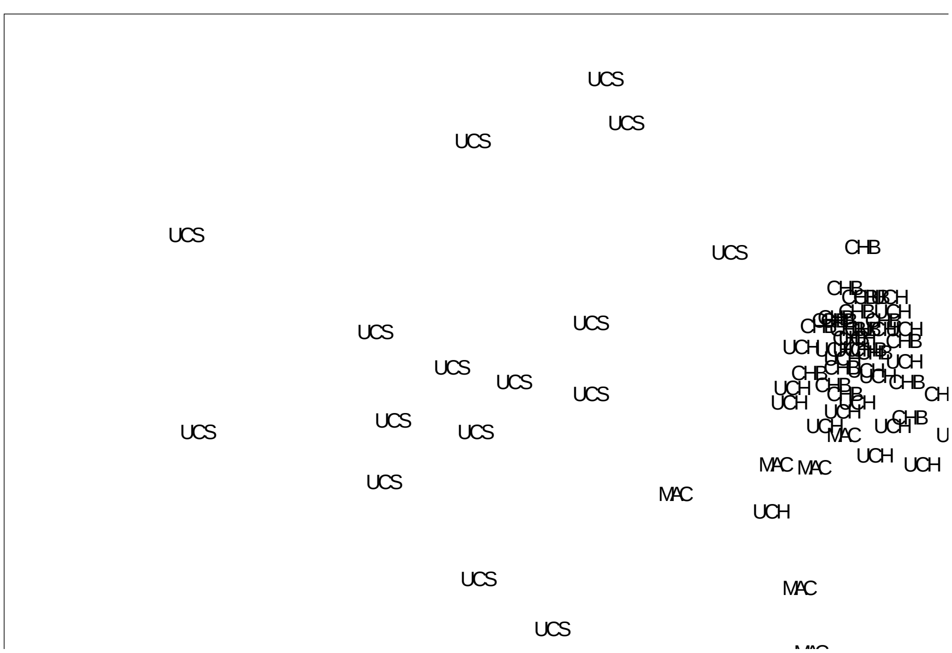

Figure 120. Nonmetric multidimensional scaling plot of sampling locations by habitat type. Input values are mean biomass (t ha^{-1}) by species for each habitat type (CHB, UCH, MAC, and UCS) and each management strata (MLCD, FMA, and open). N = 70. CHB = colonized hardbottom, UCH = uncolonized hardbottom, MAC = macroalgae, and UCS = unconsolidated sediments (sand).

Comparisons between protected areas and areas open to fishing

A ratio of fish biomass (t ha^{-1}) on hardbottom habitats inside protected areas (MLCDs and Moku o Loe) compared with outside these areas, excluding FMAs, was developed to examine how successful each protected area was relative to its adjacent habitat (Fig. 121). Biomass in the Hanauma Bay MLCD was more than eight times higher than along the adjacent south shore Oahu areas. The poor habitat quality (sedimentation and invasive seaweeds) and high fishing pressure in the areas outside the MLCD likely contribute to this large difference in biomass.

Biomass in Molokini Shoals MLCD was more than six times higher then nearby "control" areas along south Maui, but these areas may not represent true comparisons with the MLCD owing to the unique habitat of Molokini. Other MLCDs with large differences in biomass relative to their adjacent controls included: Honolua (>4 times higher), Pupukea (3.8 times higher), and Waikiki (2.5 times higher). These locations are all associated with high fishing pressure in the open areas adjacent to the MLCDs.

Waialea, Kealakekua, Lapakahi, Manele, and Old Kona Airport all had relatively small differences in the ratio of fish biomass inside the MLCD compared to the adjacent open areas. Lower fishing pressure and the good habitat quality outside the MLCDs may explain these relatively small differences.

Apex predator biomass was more than 17 times higher in these protected areas relative to areas open to fishing (Fig. 122). Primary consumer biomass was ca. four times higher in protected areas while secondary consumers showed a relatively small difference in biomass inside protected areas compared with adjacent open areas (1.7 times higher). Herbivore biomass in both protected and open areas showed a negative relationship with macroalgal cover (Fig. 123). Herbivore biomass in the MLCDs was slightly higher compared to open areas with similar macroalgae cover but these differences were not significant (ANCOVA whole model $F_{1, 23} = 2.1$, $p = 0.17$, LS Means intercept- MLCD = Open).

Factors influencing fish assemblages among all sampling locations

Stepwise multiple regression analyses were conducted to assess the importance of various independent variables on fish assemblage characteristics (species richness, biomass, and diversity). Independent variables included percent cover of live coral, macroalgae, sand, turf algae, as well as rugosity, depth, and whether the transect was protected from fishing (MLCDs and Moku o Loe Refuge) or open to fishing (open areas and FMAs).

Rugosity accounted for 50% of the variability in species richness among all sampling locations (Table 79). The presence of sand and macroalgae had negative relationships with species richness and explained an additional 13% and 3% of the variability, respectively. Protection from fishing accounted for only an additional 1% of the variance in richness.

Approximately 34% of the variability in biomass was explained by rugosity, with an additional 7% explained by protection from fishing (Table 79). Sand had a negative relationship with biomass and explained an additional 4% of the variability.

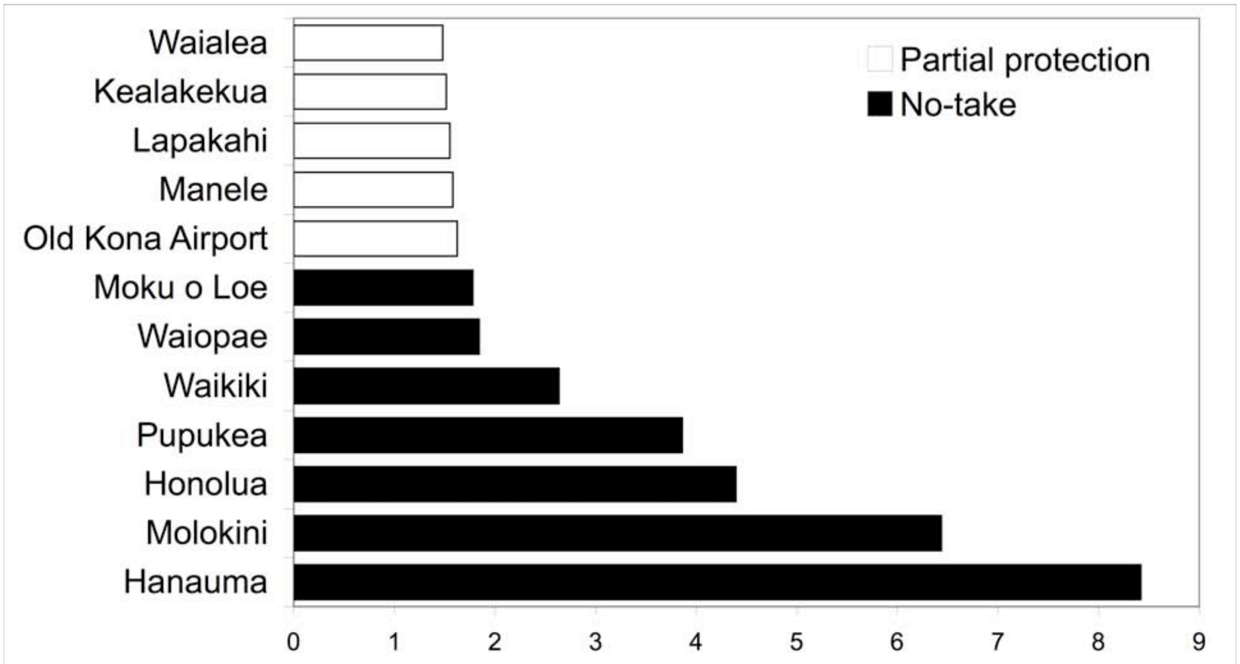

Figure 121. Ratio of biomass (t ha^{-1}) inside MLCDs and Moku o Loe Refuge vs. outside areas open to fishing. Hardbottom habitats only.

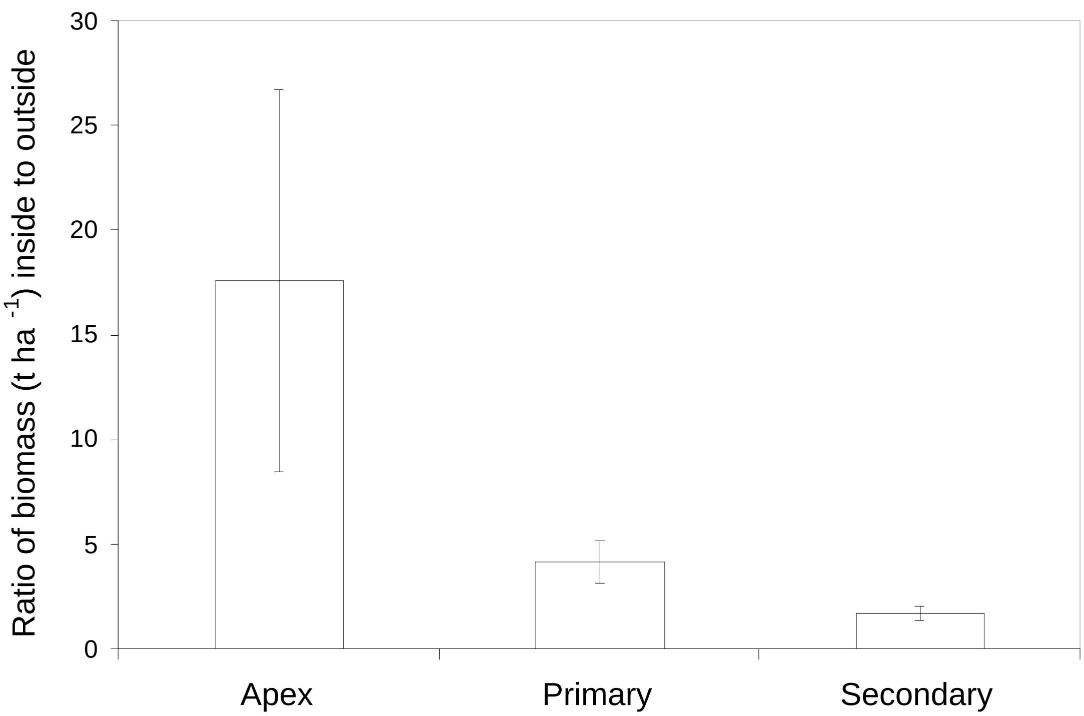

Figure 122. Ratio of biomass (t ha^{-1}) inside MLCDs and Moku o Loe to adjacent hardbottom areas open to fishing. Error bars represent standard error of the mean.

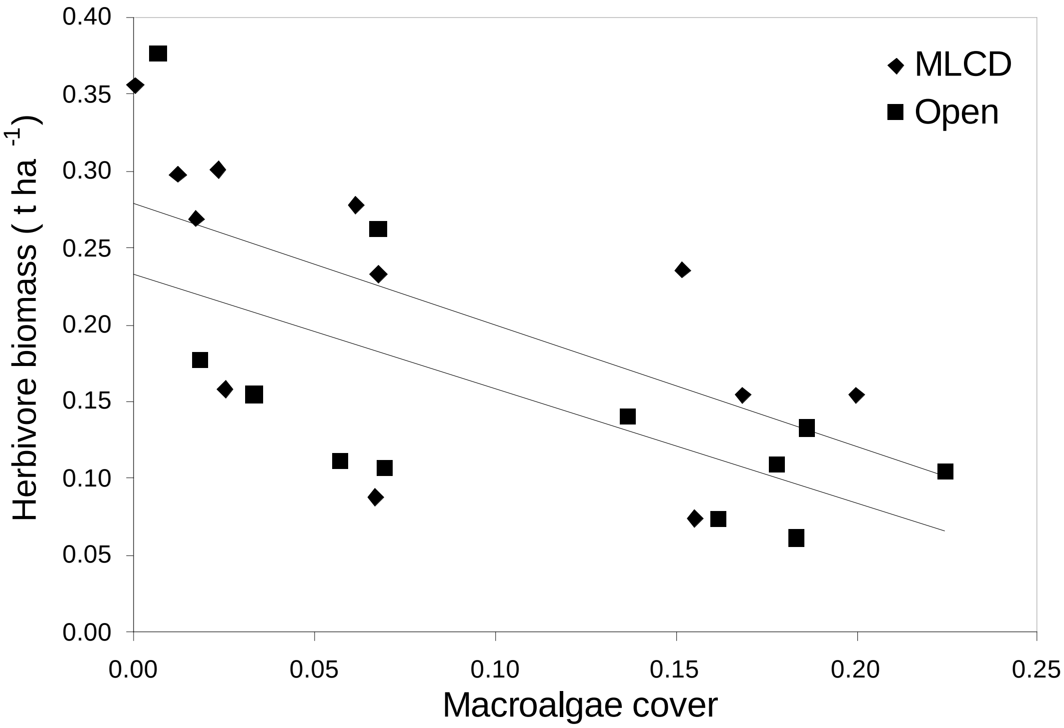

Figure 123. Comparison of mean percent macroalgae cover and mean herbivore biomass (t ha^{-1}) at protected and open areas. Macroalgae values arcsine squareroot transformed. ANCOVA model $F_{1,23} = 2.1$, $p = 0.17$, LS Means intercept - MLCD = Open.

Sand had a negative relationship with diversity and explained 54% of the variability in this assemblage characteristic (Table 79). Rugosity accounted for an additional 7% of the variability, with turf (2%), coral (2%), protection from fishing (1%), and depth (1%) contributing modest amounts to the explanatory power of the model for diversity.

On hardbottom habitats, rugosity explained 33% of the variance in species richness, 25% in biomass, and 22% in diversity (Table 80). The presence of macroalgae and sand on hardbottom habitats had a negative relationship with species richness, accounting for 9% and 6% of the variability in this assemblage characteristic, respectively. Protection from fishing explained only 4% of the variability in species richness and 1% in diversity. Protected areas did, however, account for 10% of the variability in biomass in hardbottom locations.

<u>Fish assemblage characteristics among habitat types and management regime</u>
Within major habitat types, species richness, biomass, and diversity were, in most cases, nominally higher in the MLCDs, followed by FMAs, and open areas (Table 81). Species richness was significantly higher in the MLCDs compared to open areas in all major habitats except macroalgae. Biomass in the MLCDs was significantly higher than both the FMA and open areas in all habitats except macroalgae. Among all hardbottom habitats, overall species richness and diversity were 1.4 and 1.2 times greater in MLCD and the Moku o Loe reserve compared with open areas, respectively. Overall fish biomass was 2.6 times greater in MLCDs and the Moku o Loe reserve compared with open areas.

Table 79. Stepwise multiple regression analyses for fish assemblage characteristics among all habitat types. Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion was based on Mallow's Cp criterion for selecting a model. Percent cover data were arcsin square root transformed prior to analyses.

A. Species

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.54	3999.32	149.93	41212.54	0.50	601.16
Sand	-15.34	2197.72	82.39	10452.88	0.63	211.28
Macroalgae	-7.89	650.91	24.40	2558.54	0.66	117.36
Protected-open	-1.26	1329.33	49.84	989.38	0.67	82.27
Depth	0.21	888.55	33.31	1032.88	0.68	45.55
Turf	7.79	897.56	33.65	422.52	0.69	31.71
Coral	10.83	685.77	25.71	685.76	0.70	8.00

B. Biomass

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.02	8.36	141.24	35.40	0.34	235.79
Protected-open	-0.09	6.86	115.92	7.26	0.41	115.54
Sand	-0.49	6.08	102.76	4.53	0.45	41.30

C. Diversity

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Sand	-1.20	14.75	58.14	398.24	0.55	368.88
Rugosity	0.04	18.23	71.87	50.85	0.62	170.63
Turf	1.39	29.59	116.68	19.82	0.64	94.56
Coral	1.24	9.56	37.68	12.43	0.66	47.62
Protected-open	-0.11	9.71	38.27	8.80	0.67	14.96
Depth	0.01	2.78	10.98	2.78	0.68	6.00

Table 80. Stepwise multiple regression analyses for fish assemblage characteristics on hard bottom habitats only. Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion was based on Mallow's Cp criterion for selecting a model. Percent cover data were arcsin square root transformed prior to analyses.

A. Species

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.48	3019.18	99.55	15950.27	0.33	340.14
Macroalgae	-13.36	1608.20	53.02	4358.94	0.42	198.36
Sand	-16.23	2995.63	98.77	2956.17	0.48	102.85
Depth	0.36	1622.77	53.50	1269.31	0.50	62.99
Protected-open	-1.59	1656.14	54.61	1696.86	0.53	9.01
Coral	3.97	112.12	3.70	112.12	0.54	7.31

B. Biomass

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.02	6.83	106.73	19.95	0.25	208.76
Protected-open	-0.10	7.37	115.12	8.27	0.35	81.69
Macroalgae	-0.50	2.49	38.92	2.95	0.38	37.60
Sand	-0.43	2.27	35.54	2.27	0.41	4.11

C. Diversity

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.03	10.83	48.29	63.17	0.22	242.51
Macroalgae	-0.84	5.43	24.19	23.57	0.30	139.43
Sand	-0.95	7.19	32.04	17.77	0.37	62.19
Protected-open	-0.10	6.60	29.44	4.60	0.38	43.68
Depth	0.02	5.14	22.91	6.48	0.41	16.78
Turf	0.52	2.65	11.83	1.29	0.41	13.04

Trophic composition among habitat types

The trophic structure of the colonized hardbottom habitat consisted of approximately 60% primary consumers (black durgon, surgeonfishes, and parrotfishes), 32% secondary consumers, and 9% apex predators (Fig. 124). Primary consumers comprised 72% of the biomass in the uncolonized hardbottom habitat and 54% in the macroalgae habitat. Secondary consumers (primarily triggerfishes, wrasses, and goatfishes) accounted for 45% of the biomass in the macroalgae habitat, but only comprised 26% in the uncolonized hardbottom. Apex predators comprised only 2% of the biomass in the uncolonized hardbottom habitat and 1% of the biomass in the macroalgae habitat. Although overall biomass was low in the sand habitat, apex predators accounted for 60% of the biomass in this habitat with barracuda, sharks, and jacks accounting for most of this biomass. These findings highlight the importance of this habitat for apex predators and the need to include sand habitats into reserve design.

Table 81. Comparisons of fish assemblage characteristics among management regimes by major habitat type. Values are means for all transects in each strata. Biomass = t ha^{-1}. CHB = colonized hardbottom, UCH = uncolonized hardbottom, MAC = macroalgae, and UCS = unconsolidated sediments (sand). Statistical values of One-way ANOVA for each habitat type. Unplanned multiple comparisons among management strata tested using Tukey's HSD tests. Underlined management strata are not significantly different (α = 0.05)

Species	MLCD	FMA	Open	F	p	Multiple comparisons
CHB	21.15	20.95	18.58	8.30	<0.001	MLCD FMA Open
UCH	18.44	15.00	12.85	19.50	<0.001	MLCD FMA Open
MAC	6.62	8.00	5.13	1.90	0.152	FMA MLCD Open
UCS	2.33	0.90	1.06	6.00	0.003	MLCD FMA Open

Biomass	MLCD	FMA	Open	F	p	
CHB	0.97	0.64	0.50	26.1	<0.001	MLCD FMA Open
UCH	0.87	0.39	0.30	36.7	<0.001	MLCD FMA Open
MAC	0.12	0.11	0.04	5.5	0.005	MLCD FMA Open
UCS	0.18	0.01	0.02	5.2	0.006	MLCD FMA Open

Diversity	MLCD	FMA	O	F	p	
CHB	2.19	2.24	2.06	6.30	0.002	MLCD FMA Open
UCH	2.17	2.05	1.81	13.30	<0.001	MLCD FMA Open
MAC	1.29	1.61	1.04	1.60	0.050	FMA MLCD Open
UCS	0.52	0.16	0.21	7.30	<0.001	MLCD Open FMA

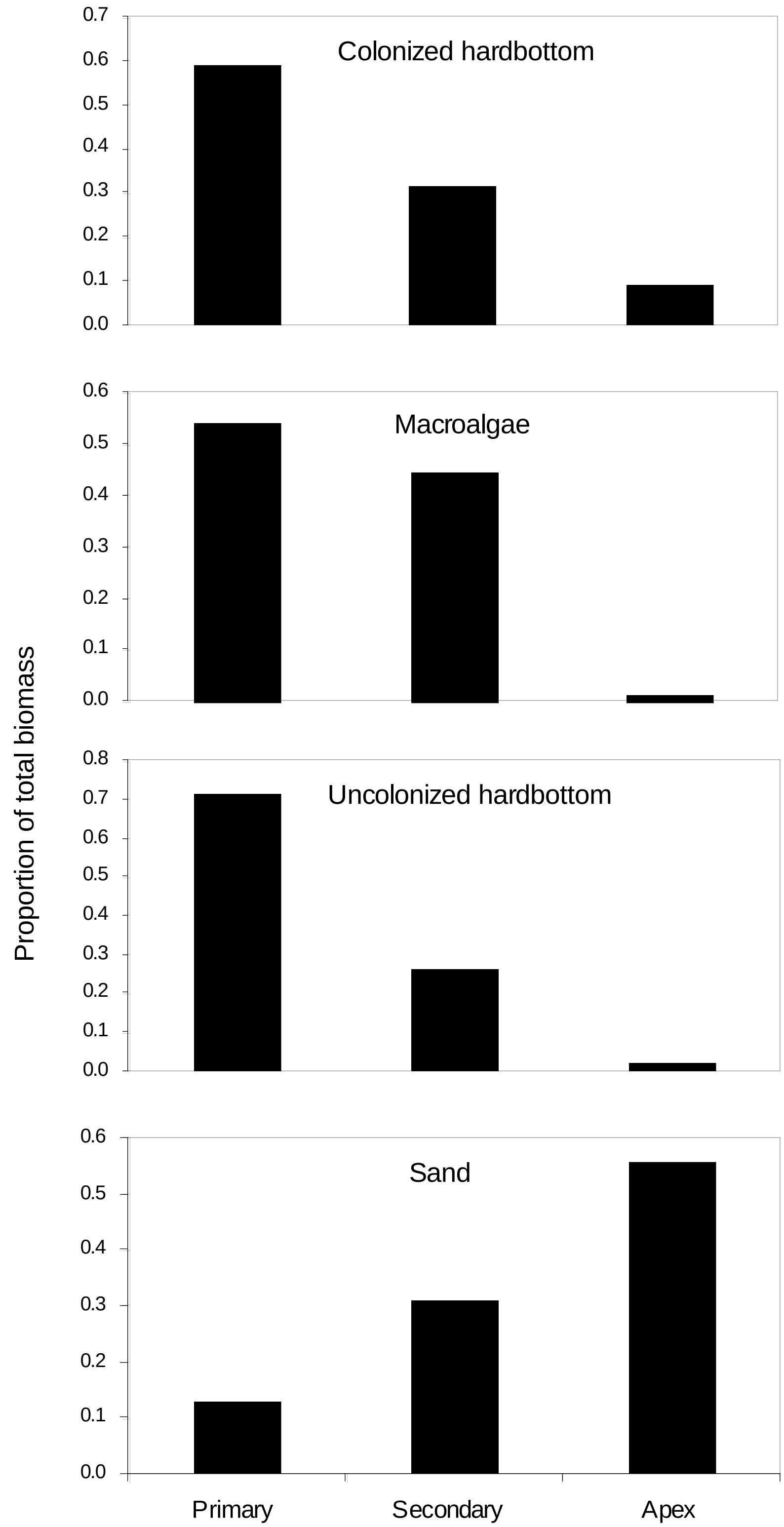

Figure 124. Trophic composition among major habitat types pooled across all locations. Proportion of total biomass among trophic guilds in each major habitat type.

Trophic composition among management regimes

Within all hardbottom habitats, biomass of primary consumers was nearly three times higher in the MLCDs and Moku o Loe compared to the open areas and twice as high as in the FMAs (Fig. 125, Table 82). Secondary consumer biomass was similar between the MLCDs and FMAs, but both were significantly higher than the open areas. Apex predator biomass was 9 times higher in the MLCDs compared with the open areas and 4.5 times higher than in the FMAs.

Size spectra among management regimes

Size spectra analysis was used to compare size structure of fish assemblages among management regimes (Fig. 126). There was a significant difference in size spectra among management regimes ($F_{2,26} = 10.4$, $p < 0.001$) with MLCDs and the Moku o Loe refuge having higher values of both slope ($p<0.05$) and intercept ($p<0.05$) compared with the other two management regimes (MLCD>FMA=Open, $\alpha = 0.05$). These results indicate that both the overall size of the adult fish assemblage was larger in the protected areas and the larger size classes had a greater number of individuals compared with the other management regimes.

Comparisons among protected areas

Old Kona Airport MLCD had a significantly greater number of species than all other protected areas (Fig. 127; Table 83). Pupukea, Lapakahi, and Honolua had the next highest species richness, but these sites did not differ significantly from Molokini, Manele, Kealakekua, or Hanauma Bay. Species richness at Waikiki, Moku o Loe, WaiOpae, and Waialea was less than half that of Old Kona Airport.

Molokini possessed the highest biomass on hardbottom among all protected areas and also had the highest biomass of apex predators (Fig. 128; Table 84.). Old Kona Airport, Kealakekua, Hanauma, Manele, and Honolua followed in biomass, respectively, and were all statistically indistinguishable from Molokini. Apex predators also tended to be most abundant in these protected areas. The lowest biomasses were recorded in the Waikiki MLCD, followed by WaiOpae, Waialea, and Moku o Loe, respectively.

Diversity was highest at Lapakahi, followed by Pupukea and Honolua, respectively (Fig. 129; Table 85). The top nine MLCDs did not differ significantly from one another in species diversity. The lowest diversity in hardbottom habitats were observed at Moku o Loe, followed by Waikiki and Waialea.

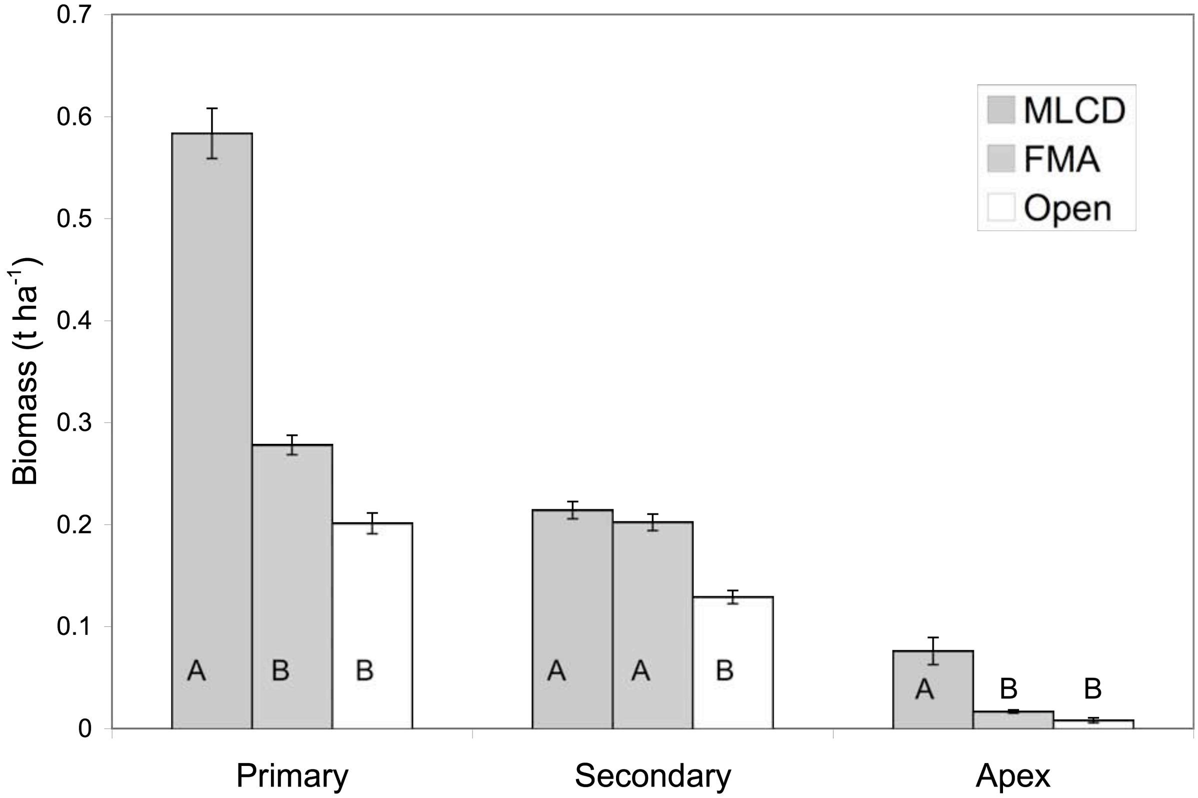

Figure 125. Mean biomass per transect (t ha^{-1}) by trophic guild and management regime on hardbottom habitats over the entire study area. Error bars are standard error of the mean. Management regimes with the same letter are not significantly different at $\alpha = 0.05$ (Tukey's HSD tests).

Multivariate comparisons among protected areas and their adjacent open access areas. Protected areas, FMAs, and open areas showed greater concordance in fish assemblage structure with each other than with other locations under similar management regimes (Fig. 130). Kaneohe Bay and Kapoho were most dissimilar from other locations sampled around the state. Kaneohe Bay is the only embayment with a barrier reef and extensive patch reefs in the main Hawaiian Islands and the assemblage structure is dominated by herbivores, especially small parrotfishes. Friedlander et al. (2003) found similar results in the only other large-scale study of fish assemblages in the main Hawaiian Islands. The Kapoho area consists of a raised lava bench that possesses a fish assemblage dominated by juveniles and small-bodied individuals. Owing to the unique habitat at these two locations, it is not surprising that the associated fish assemblages are so dissimilar to other locations in the main Hawaiian Islands. Open areas on Oahu and Maui clustered closer together in ordination space, while locations on the Kona coast of the Big Island were more similar to one another.

All protected areas, except for Waialea Bay MLCD, tended to increase along both the X and Y axes in the MDS plot relative to their corresponding open areas and FMAs. The magnitude of this shift in ordination space (Fig. 130) was correlated to the differences observed in assemblage characteristics (species richness, biomass, diversity, trophic structure, and size structure).

Table 82. Comparisons of fish biomass by trophic guild among the three management regimes pooled across all hardbottom habitat types. Statistical results of One-way ANOVAs. Unplanned multiple comparisons among management strata tested using Tukey's HSD tests (α = 0.05).

A. Primary consumers biomass

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Management	2	9.20	4.60	71.18	<0.0001
Error	749	48.43	0.06		
C. Total	751	57.63			

Comparisons for all pairs using Tukey-Kramer HSD, positive values show pairs of means that are significantly different p <0.05.

Abs(Dif)-LSD	MLCD	FMA	Open
MLCD	-	0.088	0.188
FMA	0.088	-	-0.010
Open	0.188	-0.010	-

B. Secondary consumers biomass

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Management	2	0.83	0.42	20.92	<0.0001
Error	749	14.91	0.02		
C. Total	751	15.75			

Comparisons for all pairs using Tukey-Kramer HSD, positive values show pairs of means that are significantly different at p <0.05.

Abs(Dif)-LSD	MLCD	FMA	Open
MLCD	-	-0.035	0.042
FMA	-0.035	-	0.016
Open	0.042	0.016	-

C. Apex predator biomass

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Management	2	0.33	0.18	13.38	<0.0001
Error	749	9.35	0.01		
C. Total	751	9.69			

Comparisons for all pairs using Tukey-Kramer HSD, positive values show pairs of means that are significantly different at p <0.05.

Abs(Dif)-LSD	MLCD	FMA	Open
MLCD	-	0.001	0.024
FMA	0.001	-	-0.025
Open	0.024	-0.025	-

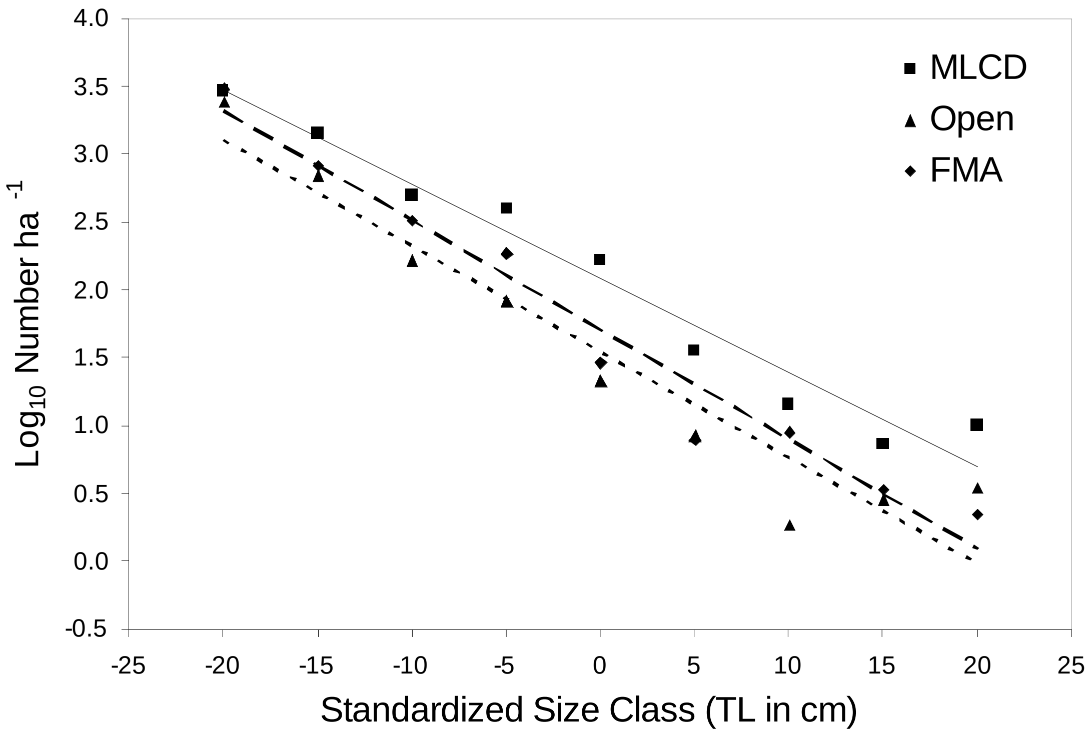

Figure 126. Size spectra of Log_{10} number ha^{-1} by standardized size class (TL in cm) for all fishes on hardbottom. ($F_{2,26} = 10.4$, $p < 0.001$, LS Means intercept - MLCD>FMA=Open, $\alpha = 0.05$)

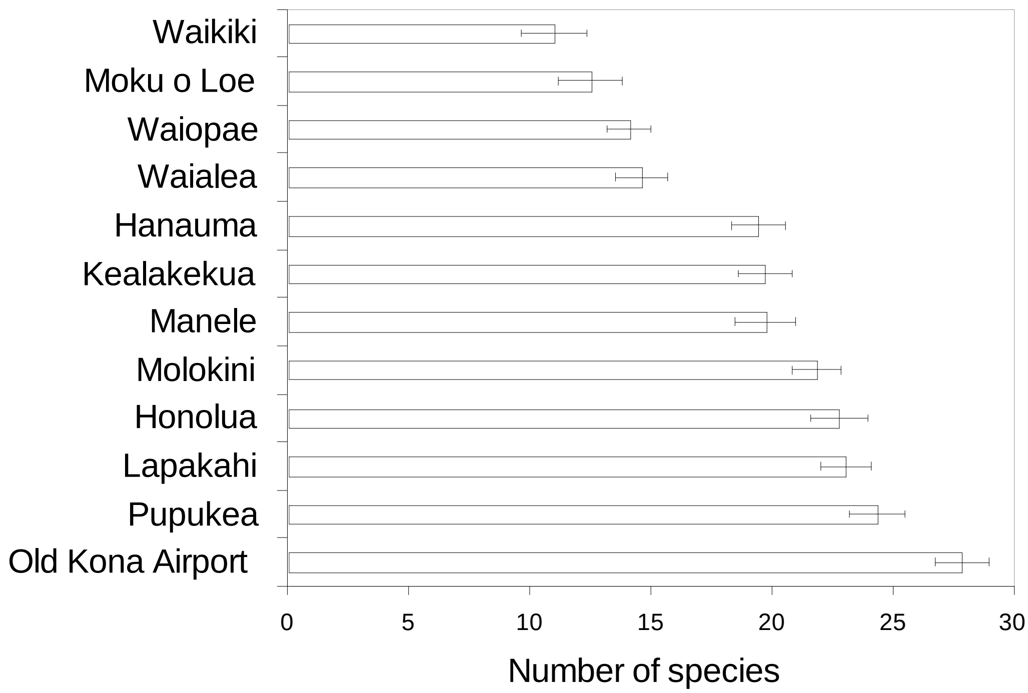

Figure 127. Mean number of species per transect (125 m^2) on hardbottom habitat only in all MLCDs and the Moku o Loe Reserve. Error bars are standard error of the mean

Table 83. Comparisons of species richness on hardbottom habitats among protected areas. Statistical results of One-way ANOVAs. Unplanned multiple comparisons among protected areas tested using Tukey's HSD tests (α = 0.05). Locations with the same letter are not significantly different.

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Location	11	7161.03	651.00	20.23	<0.0001
Error	282	9075.10	32.18		
C. Total	293	16236.14			

Location	No. species	SD	Multiple comparisons
Old Kona Airport	27.86	5.21	A
Pupukea	24.33	5.58	A B
Lapakahi	23.07	5.59	A B
Honolua	22.78	6.18	A B
Molokini	21.87	4.78	B
Manele	19.74	6.03	B C
Kealakekua	19.73	5.08	B C
Hanauma	19.45	5.22	B C
Waialea	14.63	5.27	C D
WaiOpae	14.10	4.75	D
Moku o Loe	12.50	7.27	D
Waikiki	11.00	6.16	D

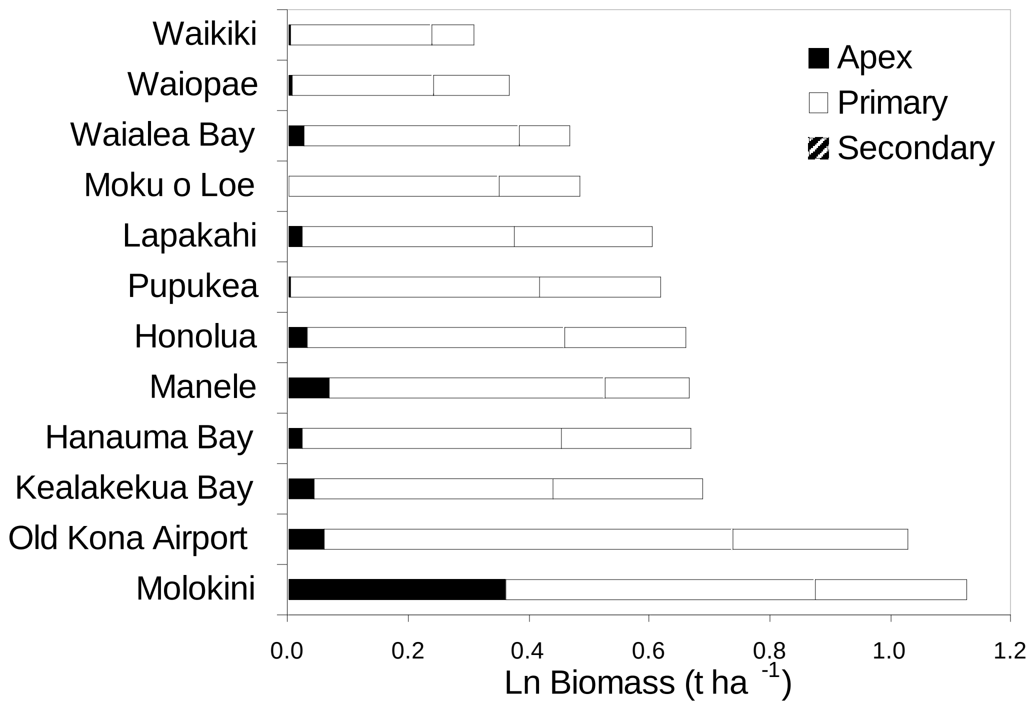

Figure 128. Mean biomass (t ha^{-1}) by trophic guild on hardbottom habitat only among all MLCDs and the Moku o Loe refuge.

Table 84. Comparisons of biomass (t ha^{-1}) on hardbottom habitats among protected areas. Statistical results of One-way ANOVAs. Biomass ln(x+1) transformed for statistical analysis. Unplanned multiple comparisons among protected areas tested using Tukey's HSD tests (α = 0.05). Locations with the same letter are not significantly different.

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Location	11	8.52	0.77	6.99	<0.0001
Error	282	31.26	0.11		
C. Total	293	39.78			

Location	Raw biomass	SD	Multiple comparisons
Molokini	1.785	1.947	A
Old Kona Airport	1.521	0.874	A B
Hanauma Bay	0.924	0.980	A B C
Kealakekua Bay	0.921	0.812	A B C
Manele	0.915	0.771	A B C
Honolua	0.896	0.721	A B C
Pupukea	0.872	0.523	B C
Lapakahi	0.744	0.347	C
Moku o Loe	0.653	0.640	C
Waialea Bay	0.620	0.591	C
WaiOpae	0.455	0.432	C
Waikiki	0.409	0.558	C

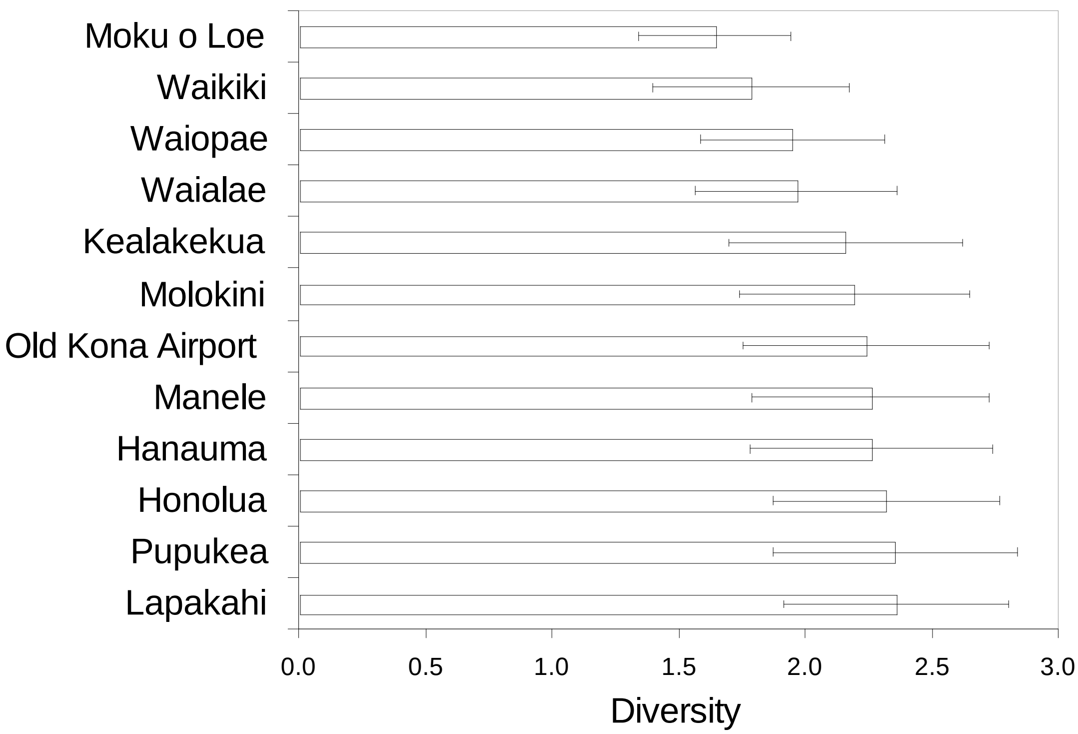

Figure 129. Mean diversity per transect (125 m^2) on hardbottom habitat only in all MLCDs and the Moku o Loe Reserve. Error bars are standard error of the mean

Table 85. Comparisons of diversity on hardbottom habitats among protected areas. Statistical results of One-way ANOVAs. Unplanned multiple comparisons among protected areas tested using Tukey's HSD tests (α = 0.05). Locations with the same letter are not significantly different.

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Location	11	15.89	1.44	7.22	<0.0001
Error	282	56.39	0.20		
C. Total	293	72.27			

Location	Diversity	SD	Multiple comparisons
Lapakahi	2.36	0.35	A
Pupukea	2.35	0.39	A B
Honolua	2.32	0.35	A B
Hanauma	2.26	0.34	A B
Manele	2.26	0.39	A B
Old Kona Airport	2.24	0.42	A B C
Molokini	2.19	0.48	A B C
Kealakekua	2.16	0.39	A B C
Waialea	1.96	0.40	A B C D
WaiOpae	1.95	0.34	B C D
Waikiki	1.78	0.63	C D
Moku o Loe	1.64	0.70	D

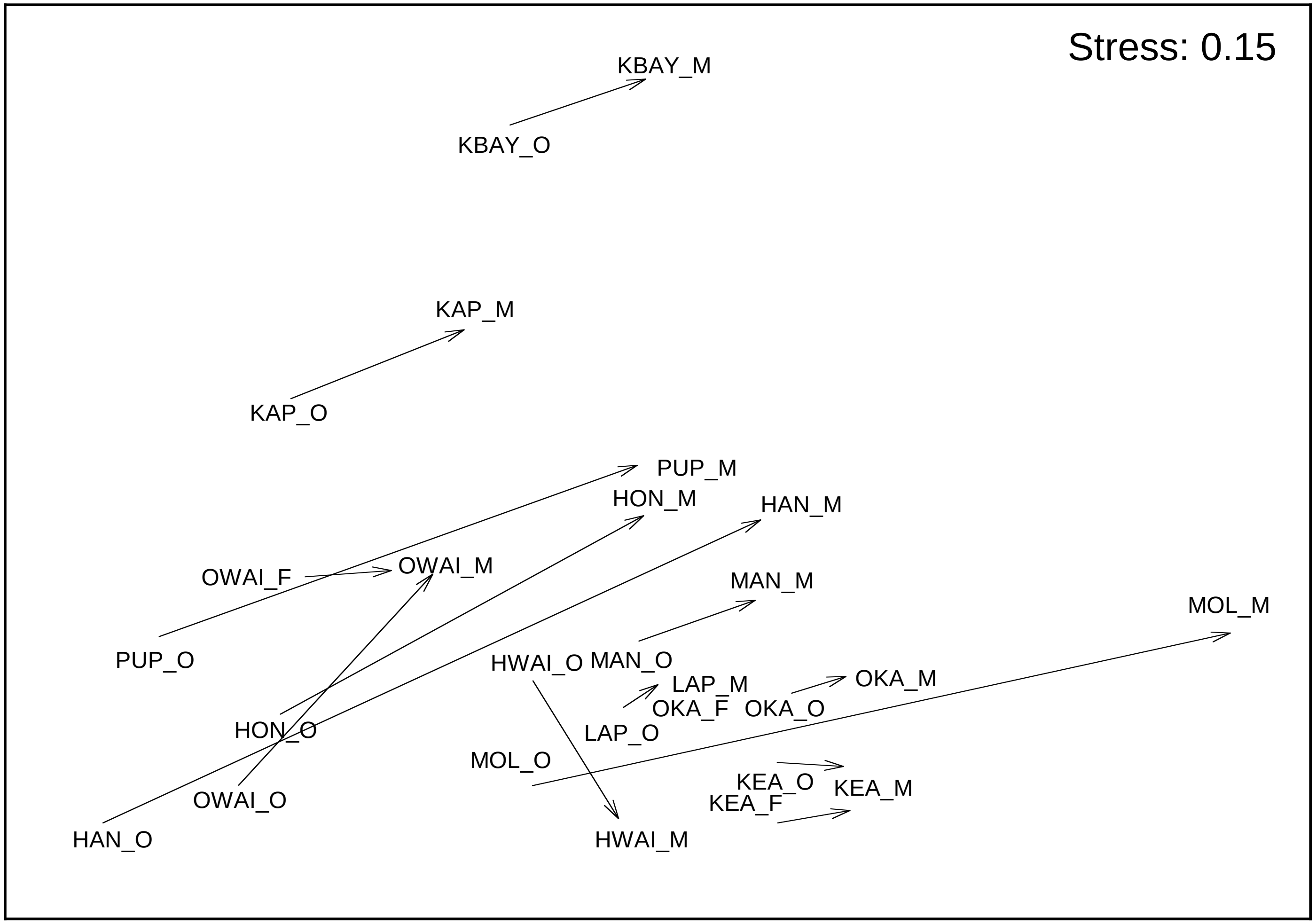

Figure 130. Nonmetric multidimensional scaling plot of mean fish biomass by species for each protected area and adjacent open areas and FMAs. HAN = Hanauma, HON = Honolua, HWAI = Hawaii-Waialea, KAP = WaiOpae (Kapoho), KBAY = Kaneohe Bay, KEA = Kealakekua, LAP = Lapakahi, MAN = Manele, MOL = Molokini, OKA = Old Kona Airport, OWAI = Oahu-Waikiki, PUP = Pupukea. MLCDs = ***_M, open areas = ***_O, FMAs = ***_F. Lines denote direction and magnitude from open area or FMA to corresponding MLCD.

General Linear Models (GLMs) among all MLCDs and the Moku o Loe refuge

To assess the contribution of benthic habitat characteristics among all MLCDs and Moku o Loe, sand habitats >1 acre MMU were excluded from these analyses because this habitat type was not found in all protected areas. Among these protected areas, rugosity was the most important parameter in explaining variability in species richness (24%), biomass (12%), and diversity 19%, Table 86). Depth explained an additional 10% of the variability in species and 2% in diversity. Sand had a negative relationship with species richness (8%) and biomass (5%). Similarly, macroalgae was negatively correlated with species richness (4%), biomass (5%), and diversity (4%). ANCOVA revealed significantly higher fish biomass in protected areas compared to open areas with similar rugosity ($F_{3,21} = 20.93$, $p < 0.001$, $R^2 = 0.78$, LS Means MLCD>Open, Fig. 131)

Mean habitat and fish assemblage characteristics were calculated on hardbottom only for each protected area to examine the large-scale habitat characteristics, integrated over the entire protected area, which explained the variability in fish assemblage characteristics at each site (Table 87). In addition to the parameters used in the models for individual transects, the total area of the protected area and the variance in depth among all hardbottom samples were incorporated into the models. Depth explained 64% of the variance in species richness and 58% in diversity over all protected areas. The presence of sand on hardbottom had a negative relationship with species richness and explained an additional 13% of the variability in this parameter. Rugosity was the only significant parameter in the biomass model and explained 52% of the variance in this parameter (Table 87).

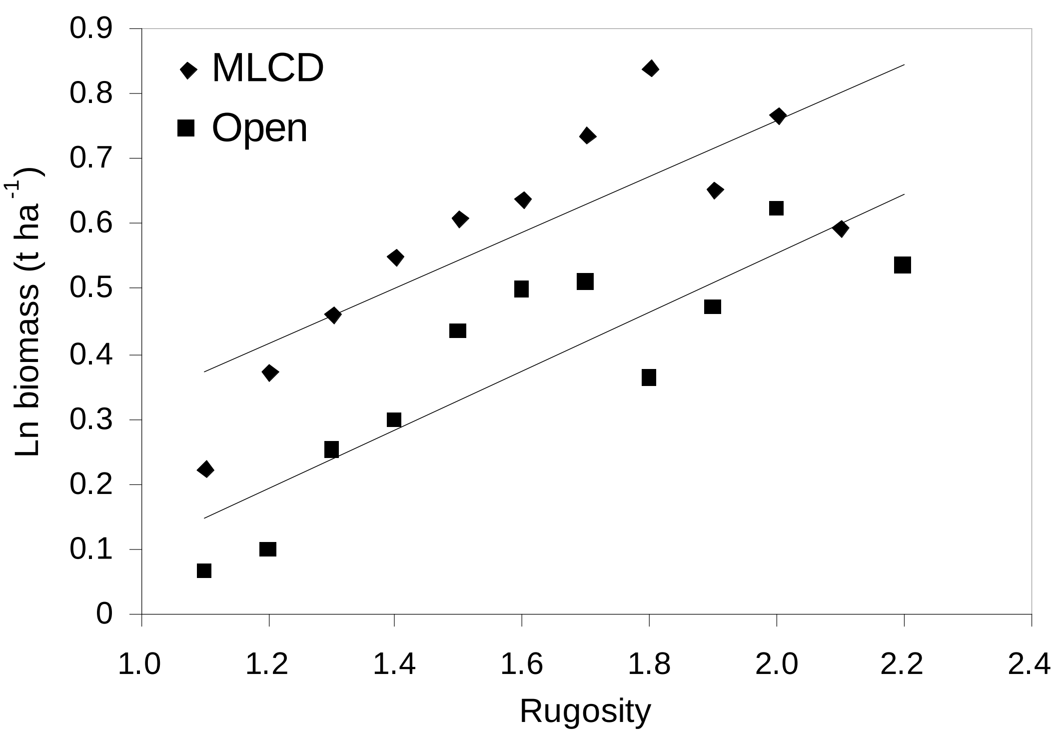

Figure 131. Comparisons of relationship between rugosity and ln biomass (t ha^{-1}) for hardbottom habitats within all MLCDs and areas open to fishing. $F_{1,21} = 24.0$, $p < 0.001$, Least Squares Means intercept – MLCD>Open, $\alpha = 0.05$).

Table 86. Stepwise multiple regression analyses for fish assemblage characteristics on hardbottom only in MLCDs and the Moku o Loe refuge. Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion was based on Mallow's Cp criterion for selecting a model. Percent cover data were arcsin square root transformed prior to analyses.

A. Species

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.463	1254.771	39.954	3832.24	0.237	103.63
Depth	0.515	852.566	27.147	1458.862	0.327	59.309
Sand	-14.550	946.919	30.152	1215.927	0.402	22.705
Macroalgae	-12.512	403.699	12.855	565.9348	0.437	6.7367

B. Biomass

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.0179	2.232	21.435	4.589	0.116	45.344
Sand	-0.696	2.393	22.988	2.189	0.171	26.404
Macroalgae	-0.979	2.662	25.564	2.142	0.225	7.917

C. Diversity

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.036	7.688	47.206	14.080	0.195	66.928
Turf	0.832	2.732	16.776	6.384	0.283	29.847
Macroalgae	-0.874	1.971	12.106	2.823	0.322	14.565
Depth	0.018	1.133	6.959	1.233	0.339	9.017

Table 87. Stepwise multiple regression analyses for mean fish assemblage characteristics and mean benthic habitat characteristics on hardbottom only in MLCDs and the Moku o Loe refuge. Additional parameters included the total area of the protected area and the variance in depth among all hardbottom samples were incorporated into the models. Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion was based on Mallow's Cp criterion for selecting a model. Percent cover data were arcsin square root transformed prior to analyses.

A. Species

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Depth	1.380	100.328	13.398	190.148	0.639	12.276
Sand	-27.567	39.960	5.336	39.9601	0.773	6.729

B. Biomass

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Rugosity	0.082	0.098	9.378	0.220	0.516	3.892

C. Diversity

Parameter	Estimate	SS	F Ratio	Seq SS	R^2	Cp
Depth	0.078	0.205	13.320	0.354291	0.5819	2.279

Discussion

Benthic assemblages varied by study site and management regime, but tended to be more similar within a study site regardless of management (e.g. Fig. 118). Overall, the most abundant substrate type was turf algae (48% cover) followed by sand (23%), coral (16%), macroalgae (7%), coralline algae (5%), macroinvertebrates (1%), and seagrasses (<1%). The Oahu sites had lower coral cover and higher macroalgal cover than the Hawaii, Lanai, and Maui sites. This pattern was most apparent at Waikiki, Pupukea, and Hanauma Bay. Coral cover was higher in the MLCDs compared to the open access areas with FMAs in between. In contrast, macroalgae cover was lowest in the MLCDs and highest in the open access areas. Macroalgal taxa appeared to account for the distinctive benthic assemblages in both the colonized and uncolonized hardbottom communities.

Analysis of benthic cover validated the *a priori* classification of habitat types and provided justification for using these habitat strata to conduct stratified random sampling and analyses of fish habitat utilization patterns. Unique fish assemblages were observed among different habitat types and among different fisheries management regimes within specific habitat types. Hardbottom habitats (colonized and uncolonized) had more species, more individuals, and higher biomass than the macroalgae habitat types and the sandy areas had few if any fish present on transects. However, valuable resource species such as bluefin trevally (*omilu*) and goatfishes (*weke*) were observed transiting these habitats and previous studies have also shown these habitats are important corridors that connect more species rich habitats. Exclusion of these habitats or other essential habitats would most certainly impose a “bottleneck” at which population and growth potential might be compromised (Christensen et al. 2003).

Rugosity was the major factor in explaining the variability in most fish assemblage characteristics, regardless of level of protection from fishing. However, when compared among areas of similar rugosity, protected areas harbored significantly greater biomass than other management regimes. Rugosity explained most of the variability in fish assemblage characteristics among protected areas on hardbottom habitat types. Mean rugosity on hardbottom habitats had the greatest influence on fish biomass within protected areas.

Protection from fishing explained approximately 10% of the variability in biomass but was not important in explaining species richness or diversity. Macroalgae and sand had negative relationships with fish assemblage characteristics. Deeper samples had higher species richness and diversity. MLCDs with deeper habitats harbored a greater number of species and higher species diversity. The protected area, FMA, and open areas within a study site showed greater concordance in fish assemblage structure than with other locations under similar management regimes.

Within major habitat types, species richness, biomass, and diversity were, in most cases, nominally higher in the MLCDs, followed by FMAs and open areas. Overall fish biomass was 2.6 times greater in MLCDs and the Moku o Loe reserve compared with open areas. The overall size of the adult fish assemblage was larger in the protected areas and the larger size classes had a greater number of individuals compared with the other management regimes. The mean ratio of apex predator biomass was more than 17 times higher in protected areas relative to adjacent areas open to fishing.

Molokini Shoals MLCD had the highest fish biomass observed among all MLCDs, followed by Old Kona Airport, Kealakekua Bay, and Hanauma Bay. Molokini also had the greatest biomass of apex predators among all areas with sharks and jacks accounting for most of the biomass. The largest difference in fish biomass between MLCDs and open areas was in the Hanauma Bay MLCD, where biomass was more than eight times higher than the adjacent open area. This difference is likely owing to the poor habitat quality (sedimentation and invasive seaweeds) and high fishing pressure in the areas outside the MLCD. In addition to having high biomass, the Old Kona Airport MLCD had the highest species richness observed on transects.

Waialea, Kealakekua, Lapakahi, Manele, and Old Kona Airport all had relatively small differences in the ratio of fish biomass inside the MLCD compared to the adjacent open areas. Lower fishing pressure and the high habitat quality outside the MLCDs may explain these relatively small differences.

Species richness, biomass, and diversity were low at Waikiki, Moku o Loe, WaiOpae, and Waialea. The small size and shallow depth range of these protected areas limit their effectiveness for biodiversity conservation and fisheries replenishment. Despite the poor habitat quality (e.g. high macroalgal cover) and small size of the Waikiki MLCD, the fish assemblage characteristics in this area were greater than adjacent areas open to fishing and the FMA, which utilizes rotational closures.

The WaiOpae MLCD consists of shallow tidepools that are dominated by juveniles and small-bodied fishes. Extension of protection into deeper water would allow for ontogenetic movement of these juveniles into deeper adult habitat.

Management Implications

Conservation and ecosystem issues will dominate fisheries management in coming years. Hopefully, this will result in managers focusing a greater amount of their efforts on conserving non-target species and ecosystems. The integration of mapping and monitoring of coral reef ecosystems and reef fish habitat utilization patterns can help managers make informed decisions about MPA design and effectiveness, as well as helping to define essential fish habitat and ecosystem function. The use of NOS digital benthic habitat maps has proven to be a powerful tool to examine the efficacy of MPAs using a spatially explicit stratified random sampling design. Analysis of benthic cover validated the *a priori* classification of habitat types and provided justification for using these habitat strata to conduct stratified random sampling and analyses of fish habitat utilization patterns based on these habitat strata.

Conclusions and recommendations

Despite the fact that marine protected areas in Hawaii have been in existence since the 1960s, up until now there has not been a comprehensive assessment of them. Findings from this study show that MLCDs protected from fishing, with high habitat complexity and good habitat quality (e.g. low macroalgae cover), have higher values for most fish assemblage characteristics. Resource species were also larger and more abundant in the MLCDs with the greatest protection from fishing and the highest habitat complexity. The inclusion of sandy habitats within MLCDs provided corridors for a number of apex predators and other vagile species, thus allowing for greater ecosystem protection. By identifying major juvenile nursery habitat types, future MPAs can be designed to maximize protection for these vulnerable life stages.

Many MLCDs in Hawaii were initially established to support the State of Hawaii's conservation and education objectives, not to enhance fish stocks. As a consequence, most of the MLCDs in Hawaii are currently too small to provide any fisheries benefits. Their small size and limited habitat types do not allow for the entire fish assemblage to function in a natural manner compared to larger and relatively pristine areas such as the northwestern Hawaiian Islands (NWHI). Mean fish biomass on hardbottom habitats in main Hawaiian Island MLCDs (0.89 t ha^{-1}) is 2.7 times less than biomass in the NWHI. The biomass of predators in protected areas is also 19 times less than those observed on unfished reefs in the NWHI (Friedlander and DeMartini 2002). MLCDs currently account for much less than 1% of the total reef area of the main Hawaiian Islands. In order for these protected areas to be self-sustaining and provide any fisheries benefits, 20-30% of the reef area needs to be protected from exploitation (Sladek Nowlis and Friedlander 2005). Self-replenishment can be achieved by reserves of sufficient size to contain a substantial amount of larval dispersal, or by networking reserves at suitable distances such that propagules produced by populations in one reserve replenish populations in other reserves. An effective reserve network design will protect populations and enhance non-protected populations through larval dispersal. MPAs in Hawaii must be larger than other tropical ecosystems because the majority of the predator biomass is mobile, such as jacks, while in other coral reef ecosystems the predator biomass consists of more resident groupers and snappers.

In addition to small size, many of the MLCDs in Hawaii do not incorporate deeper habitats that tend to have higher species richness and diversity. These deeper habitats not only enhance the biodiversity of the protected area but also protect critical habitats for larger-bodied fishes that undergo ontogenetic movements to deeper habitats with age.

Implementing a biogeographic process using GIS technology and sampling across the range of habitats present within the seascape helps to explain ecosystem connectivity and define ecologically relevant MPA boundaries (Battista and Monaco 2003). This approach aids in defining the forces that shape large-scale fish assemblage structure, and addresses specific questions about particular families of economically and ecologically important species at the scale at which management decisions are typically implemented. This design also lends itself to elucidating factors that might suggest causes for differential patterns in ontogenetic habitat selection and ergo distribution within the available seascape. Such patterns in population and community structure are necessary and fundamental components to understanding and maximizing the benefits derived from an MPA.

In summary, existing MLCDs in Hawaii vary in effectiveness relative to their habitat quality, proximity to adjacent habitats, and level of protection from fishing. Future MPA design must consider the habitat requirements and life histories of the species of interest as well as the extent of fishing pressure in the area and the degree of enforcement. If protective areas in Hawaii, and elsewhere are to be effective, they must include the diversity of habitats necessary to accommodate the wide range of fish species considered for protection. The kind of approach taken in this study, that attempts to make a functional match between habitats and fishes to be preserved, is appropriate for selection, evaluation, and management of reserves and should aid in decisions regarding existing and future MPAs.

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